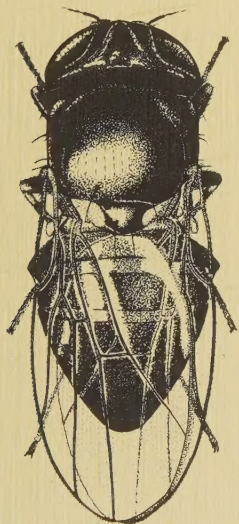


Resistance to frit fly attack in oat seedlings
An ecological approach to a plant breeding problem



Thomas Jonasson



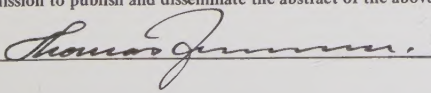
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Abstract Resistance to frit fly attack in oat seedlings is caused by two different mechanisms acting at different growth stages of the host plant. The first mechanism is associated with the interaction between the ovipositing frit fly female and the oat seedling. Seedlings are most attractive to the ovipositing females during the early stage of coleoptile separation, which normally coincides with the two-leaf stage. At this stage, the frit fly eggs can be conveniently deposited in the narrow crevice between the plant base and the coleoptile. The probability of a certain cultivar being utilized for egg-laying is approximately proportional to the duration of a suitable coleoptile crevice. Oat cultivars with thin-walled and rapidly withering coleoptiles are more liable to escape frit fly attack than are cultivars with thick-walled and persistent coleoptiles. The second mechanism of the host plant resistance pattern becomes apparent in the interaction between the penetrating frit fly larva and the seedling. Larval mortality in connection with attempts at host plant penetration varies considerably depending on cultivar and age of the seedlings. This type of resistance seems to be associated with a high density of vascular bundles in the leaf sheath, which may act as a mechanical barrier to the penetrating larvae. The total level of resistance, as observed in field experiments, is normally a sum effect of the oviposition component and the larval penetration component. Under normal conditions of cultivation, resistance to larval penetration seems to be the most important factor. Therefore, plant characters conferring penetration resistance should be given priority in attempts at breeding oat cultivars resistant to frit fly attack.			
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RESISTANCE TO FRIT FLY ATTACK IN OAT SEEDLINGS

—

AN ECOLOGICAL APPROACH TO A PLANT BREEDING PROBLEM

Thomas Jonasson

Fil. mag. Mlm

Akademisk avhandling, som för avläggande av filosofie doktorsexamen vid matematisk-naturvetenskapliga fakulteten vid Lunds universitet kommer att offentligen försvaras å Föreläsningssalen, Ekologihuset, Lund, onsdagen den 13 november 1985, kl. 0900.

182 1750. Julius Aug. Sept.

2. SLÖ-KORNS-MASKEN kallar jag et nytt Insect, på hvilket ännu ingen fedt med öppna ögon, fast det är en af de största fiender för vårt Akerbruk.

Således har jag här först föreställt et nytt eller för obekant Insect, som gör Åkermannen den största skada. Den gör vårt Fädernesland stor nytta, som kan låra oss at uteslänga detta kreaturet ifrån våra korn-åkrar.

Facsimile reproduction from "Rön om Slö-korn", the first paper dealing with frit fly damage in Sweden (Linnaeus 1750).

RESISTANCE TO FRIT FLY ATTACK IN OAT SEEDLINGS

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AN ECOLOGICAL APPROACH TO A PLANT BREEDING PROBLEM

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FM M1m

Dissertation

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ABSTRACT

Resistance to frit fly attack in oat seedlings is caused by two different mechanisms acting at different growth stages of the host plant. The first mechanism is associated with the interaction between the ovipositing frit fly female and the oat seedling. Seedlings are most attractive to the ovipositing females during the early stage of coleoptile separation, which normally coincides with the two-leaf stage. At this stage, the frit fly eggs can be conveniently deposited in the narrow crevice between the plant base and the coleoptile. The probability of a certain cultivar being utilized for egg-laying is approximately proportional to the duration of a suitable coleoptile crevice. Oat cultivars with thin-walled and rapidly withering coleoptiles are more liable to escape frit fly attack than are cultivars with thick-walled and persistent coleoptiles. The second mechanism of the host plant resistance pattern becomes apparent in the interaction between the penetrating frit fly larva and the seedling. Larval mortality in connection with attempts at host plant penetration varies considerably depending on cultivar and age of the seedlings. This type of resistance seems to be associated with a high density of vascular bundles in the leaf sheath, which may act as a mechanical barrier to the penetrating larvae. The total level of resistance, as observed in field experiments, is normally a sum effect of the oviposition component and the larval penetration component. Under normal conditions of cultivation, resistance to larval penetration seems to be the most important factor. Therefore, plant characters conferring penetration resistance should be given priority in attempts at breeding oat cultivars resistant to frit fly attack.

PREFACE

The papers included in this thesis deal with the interactions between the frit fly and oat seedling. Papers I - II treat the oviposition behaviour of the fly and the ecological significance of the host plant selection. Papers III - V deal mainly with the applied aspects and discuss the mechanisms of varietal differences in frit fly attack in oat seedlings.

The introductory part (the formal thesis) is a summary of the main results of the five papers mentioned above. It also contains however, some previously unpublished results, which I consider important in connection with a general discussion on frit fly ecology and a discussion on the possibilities of breeding oat cultivars for frit fly resistance.

During my studies on frit fly resistance in oats I have received valuable help from several persons: Gunnar Videgård and Edvard Sylén initiated the project; Hugo Andersson demonstrated frit fly damage in the field and taught me how to recognise it; Gösta Olsson and Bengt Mattsson generously put their great knowledge on cultivation and breeding of oats at my disposal; Jan Meyer gave me many practical hints regarding testing techniques in resistance breeding; Ove Hall introduced me to plant anatomy and taught me some useful techniques in connection with anatomical studies.

I also want to thank Bengt Liljedahl for taking care of most of the field trials and Ing-Britt Johanson and Yvonne Andersson for their help with the frit fly cultures in the greenhouse.

To my supervisors at the Department of Animal Ecology, University of Lund, Staffan Ulfstrand (now at Uppsala) and Per Brinck, I want to express my sincere thanks for their patience and encouragement. I also thank Per Douwes and Lars Lundqvist for reading the manuscript and giving me valuable suggestions. I'm also grateful to Ylva Zachrisson and Gunilla Lindquist for typing and editing this thesis and to Diarmuid O'Connor for correcting the language.

Finally I thank my dear wife, Monica, for accepting the frit fly as a part of our daily life.

The studies were supported by grants from Ek Hagastiftelsen, The Swedish Council for Forestry and Agricultural Research, and The Swedish Plant Breeding Board.

LIST OF PAPERS

The thesis consist of the following five papers, which will be referred to in the text by their Roman numerals.

- I. Jonasson, T. 1977. Frit fly oviposition on oat seedlings: ecological significance of the host plant selection.
- Oikos 29: 104-111
- II. Jonasson, T. 1982. Frit fly (Oscinella frit) oviposition on oat seedlings: evidence for contagious distribution of eggs.
- Ent. exp. & appl. 32: 98-100.
- III. Jonasson, T. 1980. Susceptibility of oat seedlings to oviposition by the frit fly, Oscinella frit L. (Dipt., Chloropidae).
- Z. ang. Ent. 89: 263-268.
- IV. Jonasson, T. 1982. Resistance of oat plants to larval attack by the frit fly, Oscinella frit L. (Dipt., Chloropidae).
- Z. ang. Ent. 93: 508-512.
- V. Jonasson, T. 1985. The interaction of oviposition and larval penetration in resistance to frit fly, Oscinella frit, in oat seedlings. - Manuscript.

RESISTANCE TO FRIT FLY ATTACK IN OAT SEEDLINGS - AN ECOLOGICAL APPROACH TO A PLANT BREEDING PROBLEM

THE FRIT FLY - ITS LIFE CYCLE AND PEST STATUS

The frit fly Oscinella frit (Linnaeus) is the commonest and most important stem boring pest of cereals in southern Sweden. Great economic damage occurs in oats, especially in fields where spring sowing has been delayed. The frit fly normally produces three generations a year. Flies of the first generation lay their eggs on seedlings in late spring. The larvae burrow into the shoot and start feeding at the base of the plant. The feeding activities of the larvae kill the youngest leaf. The apical meristem is also killed and consequently the shoot ceases to grow. The destroyed main shoot is normally replaced by several tillers, which start to develop soon after larval penetration. These tillers may also be attacked by late arriving flies. If unattacked however, the tillers develop normally and eventually they produce late maturing, small panicles. The larvae pupate inside the attacked shoot and in late June or early July a second generation of adult flies emerges. These flies lay their eggs in the spikelets of the young oat panicles. The larvae feed on the immature seed and pupate inside the spikelet. From these pupae a third generation of flies emerges towards the end of the summer. Adults of the third generation lay eggs mainly on tillers of wild and cultivated grasses and sometimes they also attack early sown winter cereals. Hibernation takes place in the final (third) larval instar and the larvae stay inside the host plant during the winter. An illustration of the life cycle and phenology of O. frit is given in Fig. 1.

Frit fly population build-up is rapid in oats. Southwood and Jepson (1962) estimated that the total population of adults emerging from an oat field at the end of the season, after two generations, was at least two hundred times as dense as the initial ovipositing population in the spring.

The economic damage caused by frit fly attack in oats is difficult to estimate on the basis of the frequency of attacked plants, since there is probably some compensatory growth in healthy plants growing adjacent to attacked ones. Larsson (1984) reported an average yield increase of 15 % after two applications of insecticides in a series of small scale field trials in southern Sweden. In regions where heavy attacks often occur, especially in the province of Småland, yield losses may be even greater. Sinander and Andersson (1979) reported over 30 % attacked main shoots in two consecutive years from a study in southern Småland.

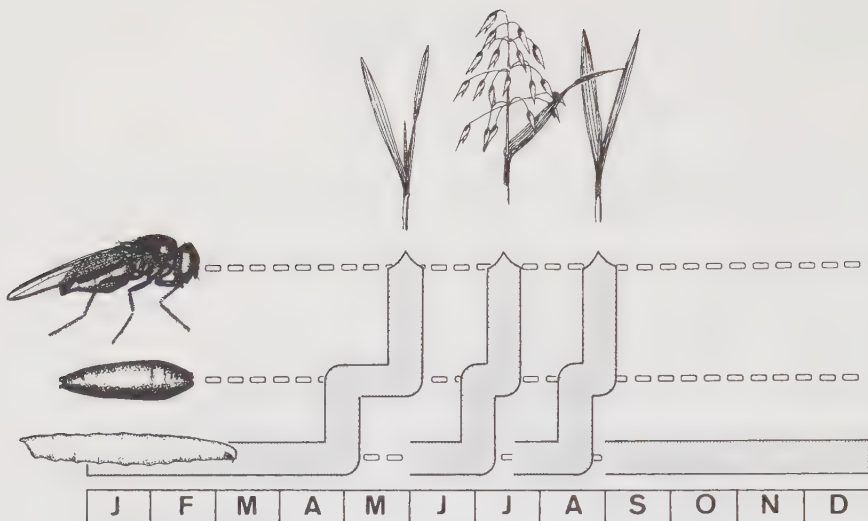


Figure 1. Frit fly phenology under normal conditions in southern Sweden. The developmental time is indicated at three levels, from bottom to top representing the larval, pupal, and adult stages. The oviposition targets in top of the illustration are, from left to right, an oat seedling, an oat panicle and a wild grass shoot (or an early sown winter cereal seedling) (from Jonasson 1975).

If the oat plants have passed the four-leaf stage before the population of flies is at its peak, the risk of an attack is low. Early sowing in the spring, therefore, is a good precautionary measure against frit fly and also the cheapest way of minimizing the risk of an attack. In some regions of southern Sweden however, spring sowing is often delayed due to wet soil conditions and therefore use of chemical control measures have become more widespread. The best results seem to be achieved by means of an early application of synthetic pyrethroids (Larsson 1984). A review of chemical control methods of the "pre-pyrethroid era" is given by Larsson (1984).

Due to the lack of suitable methods of predicting the time of oviposition in *O. frit*, it is difficult to estimate accurately the need of applications of insecticides. To be on the safe side, many farmers use chemical control methods as a routine practice. As a consequence, the use of insecticides in frit fly control has increased dramatically during the last few years.

The oat crop may suffer twice from frit fly attacks during the growing season - both in the seedling stage and in the panicle stage. Panicle attack seems to be highly associated with seedling attack, since a successful control of flies attacking seedlings also reduces the panicle attack (Riches 1960, Larsson 1984). The seedling attack therefore should be regarded as the most important one. The strategy of frit fly control should be to reduce the population of larvae attacking the seedlings. Consequently, breeding for frit fly resistance in oats should be applied to the seedling stage and not the panicle stage. Fortunately, there seems to be a broad range of variation in susceptibility at the seedling stage among oat cultivars. This raises hopes for developing successful breeding programmes in the future. There is indeed a wide variation in susceptibility to attack in the panicle stage also, but the varietal differences are mainly due to different degrees of synchronization between panicle burst and frit fly activity. Oat cultivars with early panicle development usually escape heavy attacks (Riches 1960, Jonasson 1976). It should be emphasized however, that early panicle burst in oats is normally associated with a lowered yielding capacity (Wiklund 1968).

THE LIFE TACTICS OF THE FRIT FLY

Many insect pests are opportunistic species. Often with a good migratory ability, they exploit a resource, e.g. a sprouting crop, by colonizing it rapidly. After utilizing the resource as food for one or more rapidly developing offspring generations, they leave it when it is exhausted or when competition becomes severe (Price 1975).

Several of the attributes of a successful opportunist can be found in O. frit. The good migratory ability is achieved by a combination of active flight and a passive transportation by wind currents at high altitudes (Southwood et al. 1961, Johnson et al. 1962). Another trait of an opportunist is a broad exploitation pattern (Price 1975). The host plant range of O. frit comprises most wild and cultivated grasses including cereals and maize. According to Heinicke (1978) about 60 species of Poaceae have been recorded as host plants. The only cultivated grass species not attacked by O. frit seems to be Dactylis glomerata. A third character found in O. frit and typical for an opportunistic species is a rapid larval development. In central western Europe and southern Scandinavia the common frit fly normally produces three generations a year.

Nielsen and Nielsen (1984) have presented very interesting ecological data concerning O. frit and O. pusilla (Meigen), two chloropids common in Danish grasslands. Their results indicate different evolutionary trends in the two morphologically very similar species and support the view that O. frit is an opportunistic species, at least in comparison with O. pusilla. O. frit strongly dominated in new habitats but its frequency relative to O. pusilla gradually decreased in more mature grassland ecosystems (Tab. 1).

Table 1. Relative proportions of Oscinella frit and O. pusilla in Danish grasslands of different ages. The results are based on watertrap catches reported by Nielsen and Nielsen (1984).

Crop	% <u>O. frit</u>	% <u>O. pusilla</u>
Annual or newly sown fields of <u>Lolium</u> spp.	99	1
Perennial mown grass fields	78	22
Old perennial grassfields, e.g. pastures	61	39

Nielsen and Nielsen (1984) also found that in a very old grazing pasture (unploughed for 25 years) O. frit emerged in very small numbers, while O. pusilla was common (4 and 92 individuals per m², respectively). According to the same authors, isolated patches of grass in woodland were inhabited solely by O. pusilla. Nielsen and Nielsen (1984) also found that O. frit was highly migratory, while O. pusilla was stationary. Another interesting difference is that O. frit produces three generations a year compared to only two in O. pusilla.

OVIPOSITION BEHAVIOUR

The frit fly strongly prefers to lay eggs in the narrow crevice behind the loose coleoptile of cereal seedlings (Riggert 1935, Andersson 1956, Sanders 1960, Jones 1969, Heinicke 1978). This preference is demonstrated by a very characteristic and stereotyped behaviour. Turning spirally up and down the plant base, with the extended, soft ovipositor trailing on the plant surface, the female investigates the coleoptile region in great detail to find a suitable egg-laying site (Fig. 2 A). The tip of the ovipositor is turned from side to side (Fig. 2 B) until a firm support is found. The inner surface of the coleoptile apex is the main target of this examination. Normally the narrow crevice between the coleoptile and the leaf sheath base offers an acceptable support for the ovipositor and the egg can be deposited there (Fig. 2 C).

Most studies on the oviposition behaviour of O. frit have been focused on the interaction between the frit fly female and the young host plant seedling. However, by using the same repertoire of searching behaviour, the fly is also capable of finding suitable oviposition sites on tillers and panicles of the oat plant. On a tiller the female normally oviposits behind the basal leaf sheath, a structure which strongly resembles the coleoptile of a young seedling. In the panicles, eggs are deposited inside the glumes of the spikelets.

In the oat field there are two alternative types of egg laying sites available to frit flies emerging in early July: Tillers and panicle spikelets. The tillers may be produced spontaneously by healthy oat plants if the supply of light, nutrients, and water is sufficient. Tillers may also be produced by plants previously attacked by frit fly larvae, as a response to the attack. The number of potential breeding sites is far greater in the panicles than in the tillers, so a true opportunist would probably choose the panicles. Both the panicles and the tillers are utilized, however, by the egg-laying female flies. Specimens collected in the field while laying eggs in oat panicles readily switch over to a typical "coleoptile egg-laying behaviour", if they are confined to young oat seedlings in a laboratory cage (Jonasson unpubl.).

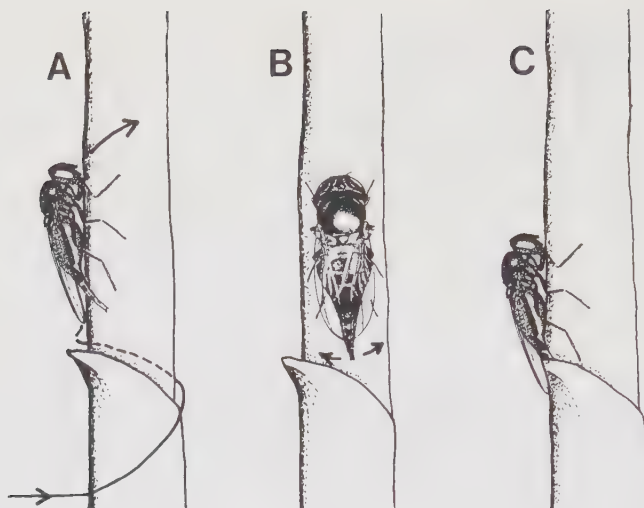


Figure 2. Different phases of the oviposition behaviour of O. frit. For details, see text.

THE EXPLOITATION OF OAT PANICLES - A RECENT ADAPTATION IN O. FRIT?

The broad exploitation pattern of the frit fly is well demonstrated by its ability to attack both tillers and panicles of the oat plant. From an evolutionary point of view, the panicle attack is particularly interesting. Very few wild grass species in northern Europe have seeds large enough to support a developing frit fly larva. Therefore it seems improbable that seed attacks in "natural" ecosystems are of any significance.

In a late sown oat field at Svalöf puparia were collected from attacked tillers and attacked panicles simultaneously (Jonasson unpubl.). In puparia collected from tillers, a high frequency of predation by parasitic wasps was observed. Some specimens of the saprophagous chloropid Elachiptera cornuta (Fallén), which often feeds inside plants attacked by phytophagous chloropids, were also found among the tiller puparia. From the material collected in panicles, however, only O. frit hatched (Tab. 2).

Table 2. Hatching of chloropids and parasitic Hymenoptera from puparia collected from tillers and panicles in an oat field at Svalöf (unpubl. data).

Hatching species	Tillers		Panicles	
	Nos.	%	Nos.	%
Chloropidae ¹⁾				
<u>Oscinella frit</u> (Linnaeus)	18	23	60	75
<u>Elachiptera cornuta</u> (Fallén)	9	11	0	0
Parasitic Hymenoptera ²⁾				
<u>Hexacola hexatoma</u> (Hartig)	5	6	0	0
<u>Cyrtogaster vulgaris</u> (Walker)	4	5	0	0
<u>Callitula bicolor</u> Spinola	3	4	0	0
<u>Spalangia fuscipes</u> Nees	3	4	0	0
<u>Halicoptera circulus</u> (Walker)	2	2	0	0
Unhatched puparia	36	45	20	25
Total	80	100	80	100

1) Det. Hugo Andersson. 2) Det. Göran Nordlander.

A low frequency of predation by parasitic wasps in the panicle generation of O. frit has been observed by several authors (see Jones 1968 and Nordlander 1978 for references). Jones (1968) assumed that lacking synchronization in development between predator and prey was responsible for this effect. In some species of parasitoids it may be true, but for others it cannot be the case (Tab. 2). Instead it seems more probable that the searching behaviour of the parasitoids near the ground (Nordlander 1978) makes the panicle puparia escape predation. The fact that most parasitoids have not succeeded in coping with frit fly larvae and pupae in the panicles strongly indicates that the exploitation of the oat panicles is a comparatively recent adaptation in O. frit.

PROBLEMS ASSOCIATED WITH THE SEEDLING ATTACK

Cunliffe et al. (1925) exposed oat plants of different stages of growth to a natural frit fly population and found that the probability of the main shoots being attacked was maximal during the two- and three-leaf stages. "Plants in the early one-leaf stage", they concluded, "showed a certain degree of immunity, due to size non-attractiveness". That old oat shoots are seldom attacked by frit fly larvae is a well known fact. An old shoot

is more resistant to penetration by the larvae than a young shoot. Why then are very young, easily penetrated plants avoided by the ovipositing females? Being an opportunist, O. frit should be utilizing a new resource as quickly as possible. In an experiment with different developmental stages of oat plants, each being artificially provided with one frit fly egg, I examined the interrelations of the frit fly larva and its host plant (I). The results showed that larval penetration into the host was most successful in the youngest plants. Older plants were after a certain age impossible to penetrate (Fig. 3 A). On the other hand, the ability of the shoot to support a growing larva was poor in young plants. This was demonstrated by a tendency of the larvae to leave the exhausted main shoot and enter newly formed tillers (Fig. 3 B). Although the larvae were able to move within the plant and hence avoid starvation, survival was lower in very young plants than in older ones (Tab. 3 C). To sum up, quality and quantity of the host plants are two conflicting properties which determine the probability of survival of the frit fly larvae.

While a growing oat plant is soon impossible to penetrate, a very young plant offers an insufficient supply of food. According to the results reported (I), larvae hatching from eggs laid on plants in the two-leaf stage had achieved an optimal compromise between the risk of not being able to penetrate the host plant and the risk of over-exploiting it. Therefore, to maximize her fitness, the frit fly female has to lay her eggs on plants at that stage, which seems to coincide fairly well with the coleoptile separation phase (Fig. 3 D).

ECOLOGICAL SIGNIFICANCE OF THE OVIPOSITION BEHAVIOUR

The oviposition behaviour of the frit fly indicates that a narrow crevice (a hiding place for the egg) plays an important role in the selection of egg-laying sites. But not just any narrow slit gives a sufficiently strong stimulus. In experiments with various artificial oviposition targets, I demonstrated that the tactile stimulus from a narrow crevice and a chemical stimulus from the host plant must act simultaneously on the female to elicit oviposition (I, II). Similar results were reported by Heinicke (1978). Close connection between the components of the total stimulus pattern affecting the frit fly female obviously enhances the survival of frit fly progeny. If a simultaneous reception by the female of a tactile stimulus from the coleoptile crevice and a chemical stimulus from the leaf

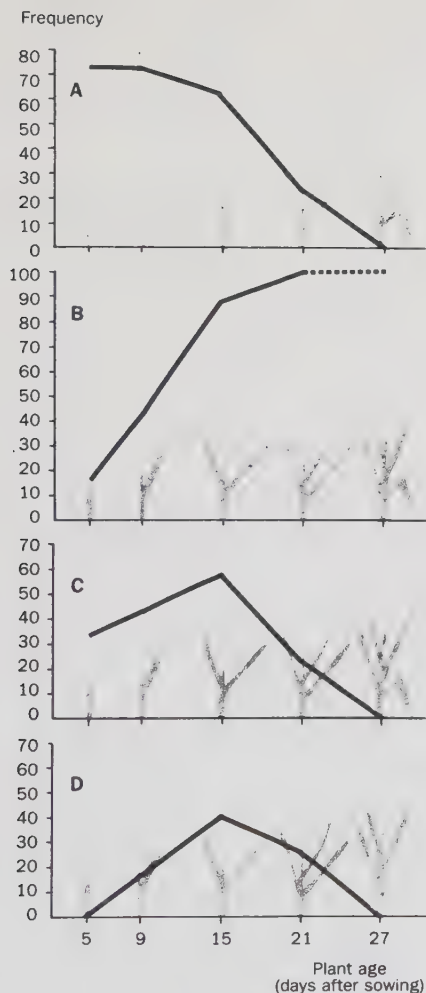


Figure 3. The relationship between different developmental stages of oat plants (cv. Victory) and penetration success and survival of frit fly larvae. A) Frequency (%) of successful penetrations. B) Frequency (%) of penetrating larvae staying inside the attacked main shoot. C) Frequency (%) of surviving larvae. These results are based on total numbers of larvae, including those moving from an exhausted main shoot to a tiller. D) Frequency (%) of plants with coleoptiles detached but not wilted = suitable for oviposition. (A-C from Jonasson 1977, D unpublished data).-

sheath base is required to release oviposition, she will be prevented from laying her eggs on the smooth surface of leaves and straw, where the eggs might easily be dislodged by a rain shower. Nor will she straggle away from the plant and hence have to oviposit in the soil, where the eggs or the larvae may be detected by predators.

The behaviour of a frit fly examining a potential host plant is very similar to that of the cabbage root fly (Delia brassicae Bouché) as described by Zohren (1968). The "stem-run" of D. brassicae on a crucifer plant seems to be very similar to the searching movements of D. frit at the base of an oat seedling. Miller and Strickler (1984) discussed the biological significance of the intricate behaviour of D. brassicae and suggested that females during the phases of close contact with the host plant, i.e. the stem-run, probably are receiving strong olfactory stimulation via antennae and gustatory stimulation via taste receptors on the tarsi as well as on the mouthparts. In addition to the chemical stimuli, visual scanning could occur during these phases and the movements around the stem might yield information on resource size.

The localization of an egg-laying site is a time-consuming task for the frit fly female. Plants without a suitable crevice behind the coleoptile may be abandoned after a lengthy procedure of investigation. Otherwise, after many abortive attempts, the female lays her eggs in the soil at the plant base (I). Searching time and number of investigated plants before oviposition in a greenhouse experiment are given in Tab. 3.

Table 3. Searching time and number of investigated plants before oviposition in two groups of frit fly females confined to A) young and B) old oat seedlings. ** = $P < 0.01$, *** = $P < 0.001$, S.E.M. = Standard Error of the Mean (Data from I).

Growth stage	No. of obs.	Searching time (min)	No. of plants investigated
		before the egg was laid	before the egg was laid
		Mean $\pm$ S.E.M.	Mean $\pm$ S.E.M.
A) Young seedlings; few coleoptiles detached	20	8.3 $\pm$ 1.45	3.8 $\pm$ 0.70
B) Old seedlings; many coleoptiles detached	20	3.2 $\pm$ 0.37	1.2 $\pm$ 0.12
Test of significance		$t_{(38)} = 3.44$ **	$t_{(38)} = 3.67$ ***

The frit fly usually deposits only one egg at a time. Plants with attractive coleoptiles may be visited repeatedly by several females however, and therefore multiple ovipositions on the same plant may occur (II). There seems to be no mechanisms that enable the female to avoid a plant already occupied by a frit fly egg. On the contrary, a tendency of contagious distribution of eggs can be observed. Considering the limited food supply provided by a young plant, oviposition on an already occupied plant seems to be a wasteful strategy for the frit fly female. However, since the larvae are able to move from an overcrowded main shoot to a tiller, the disadvantage of multiple oviposition is reduced, i.e. the secondary dispersal by the larvae may compensate for the tendency of the females to aggregate the eggs (II).

MORTALITY FACTORS IN EGG AND LARVAL STAGES

Eggs deposited behind the coleoptile are well protected against predators and desiccation. In a small field experiment with different degrees of exposure of frit fly eggs it was shown that eggs and/or larvae hatching from eggs behind the coleoptile had a lower mortality than eggs and/or larvae placed in the soil near the plant base (I). From these results a mortality rate about 40 % due mainly to predation and desiccation can be calculated for the "soil eggs". The corresponding figure for "coleoptile eggs" was less than 10 %. Hence, oviposition at protected sites certainly would be selected for in O. frit. Compared with other possible hiding places for the eggs on a young oat plant, the coleoptile crevice may give an additional selective advantage: Larvae hatching behind the coleoptile, near the plant base, have a short way to penetrate before they reach the meristematic region, where feeding takes place.

An important mortality factor acting on newly hatched larvae is related to the resistance of the host plant. In the field experiment referred to above (I), about 30 % of the larvae died because they were unable to invade the plant. As can be seen in Fig. 3 A, larval mortality due to host plant resistance varies between 30 % and 100 % depending on the age of the plant. In a field study on the ecology of O. frit in the oat crop, Southwood and Jepson (1962) suggested that the key mortality factor was connected to the time before the larvae enter the plant. This mortality could be due to egg predators, but only very small numbers of possible predators were found. Southwood and Jepson (1962) therefore concluded that the most important mortality factor besides non-viable eggs was failure of the larvae to invade the host.

MECHANISMS OF RESISTANCE TO FRIT FLY ATTACK IN OAT SEEDLINGS

A) RESISTANCE TO OVIPOSITION

A close relationship between attractivity for oviposition and susceptibility to frit fly attack among oat cultivars has been pointed out by several authors (Cunliffe and Hodges 1946, Bingham and Lupton 1958, Peregrine and Catling 1967). The egg laying behaviour of the female fly is very much focused on the coleoptile of the host plant seedling (see above). The coleoptile is the first part of a germinating oat seedling to emerge above the soil surface. From inside this parenchymatous closed tube the first leaf of the plant develops. As the leaf grows, the apical part of the coleoptile is broken through and the remnants form a tight fitting sheath around the leaf base. The coleoptile is, however, an ephemeral structure which soon loses its firmness and begins to detach from the plant. The apex is bent outwards, and a gradually expanding crevice along the plant base is formed until, finally, the coleoptile withers. Andersson (1956) reported that differences in oviposition attractivity in oats were largely due to differences in the length of the period during which the coleoptile offered a suitable site for oviposition. I similarly reported experimental data showing a good correlation between the pattern of coleoptile development and the relative susceptibility to field attack in a set of late sown oat cultivars (III). A laboratory study also showed that the frit fly females were able to locate the suitable oviposition sites very efficiently; there was a very good correlation between coleoptile appearance and oviposition frequency (Fig. 4).

Among the cultivars tested, there were a few showing morphological characters considered by Andersson (1956) to be important in connection with resistance to frit fly oviposition, viz. red shoot bases and/or hairy leaf sheaths. The close relationship between coleoptile appearance and egg-laying (Fig. 4) indicates however, that the influence of these plant characters must have been small. The key factor in determining oviposition attractivity seems to be the pattern of coleoptile development.

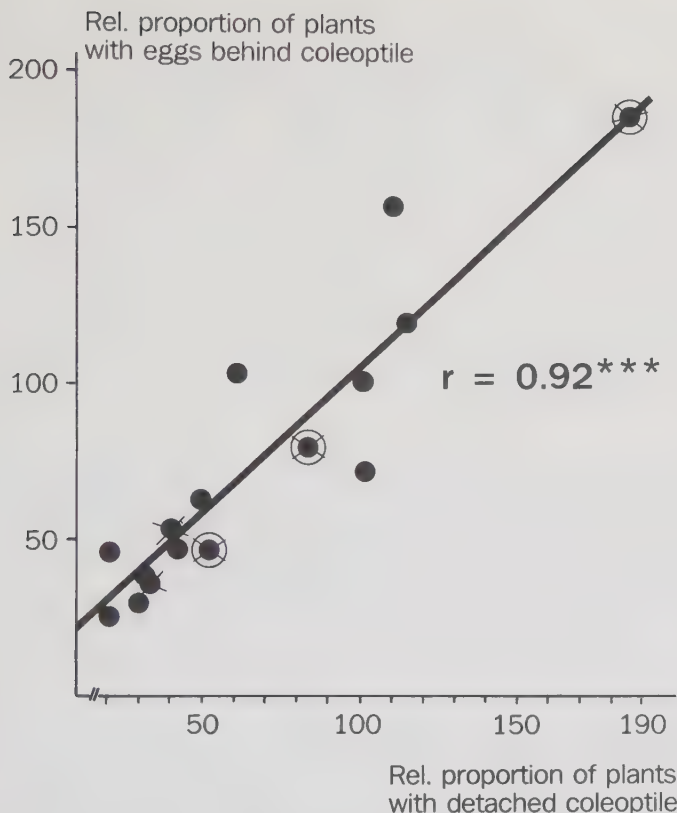


Figure 4. The relationship between proportions of detached coleoptiles and proportions of plants with eggs behind the coleoptile in 16 oat cultivars. Encircled dots = cultivars with red shoot bases; Crossed dots = cultivars with hairy shoot bases (Data from III).

B) RESISTANCE TO LARVAL PENETRATION

From the egg hidden behind the loose coleoptile, an agile larva hatches, which burrows into the shoot and enters the meristematic region. With increasing age the oat shoot becomes more resistant to larval attack (Fig. 3 A). The gradually increasing resistance to penetration seems to be a general tendency in all oat cultivars. Some cultivars, however, obviously acquire this type of resistance more rapidly than others. The old local variety Gotland oats shows a rapidly evolving resistance to larval penetration, whilst in cvs Hede, Spet, and Summer the rate of increase is much slower (IV, V).

One reason for oat plants becoming more resistant to larval attack with increasing age may be the general growth of the plant. The pseudostem of an oat seedling consists of layers of leaf sheaths tightly rolled together. It seems reasonable to suggest that it is more difficult for the newly hatched larva to penetrate the plant base if it consists of many layers of leaf sheaths than if it consists of a few. This mechanism can hardly explain differences in resistance to larval penetration, however, since the number of leaf sheaths varies very little among cultivars in early developmental stages. Among eight cultivars studied (unpubl. data) there was some variation in plant base diameter but the correlation between this character and larval penetration was weak ($r = -0.18$; n.s.; cf. Tab. 4).

Another factor more likely to be involved in resistance to larval penetration is the density of vascular bundles in the leaf sheaths. According to Moore (1984), mechanical properties of the grass stem are of considerable importance in determining whether it is penetrated by frit fly larvae or not. Cunliffe (1936) suggested that differences in frit fly attack may be due to differences in crude fibre production. According to Blum (1968), resistance to larval attack by the sorghum shoot fly (Atherigona varia soccata Rond.), a stem borer ecologically similar to the frit fly, is associated with a high degree of lignification of the cells enclosing the vascular bundle sheaths within the central whorl of the young sorghum leaves. An anatomical study of the oat seedlings (Tab. 4) showed that the most resistant cultivars had the highest numbers of vascular bundles. There was a strong negative correlation ($r = -0.89$; $P < 0.01$) between frequencies of vascular bundles and larval penetration in the cultivars studied.

The indication of a relationship between the density of vascular bundles and resistance to larval attack (Tab. 4) justified a preliminary investigation on the effect of selections based on this simple anatomical character. A total of 443 plants from a segregating F_2 population derived from a (Gotland x Sang) x Sv 80384 cross were cultivated in a peat soil mixture in the greenhouse. At the three-leaf stage, the first leaf sheath of all plants was cut off just above the coleoptile apex. The leaf sheath sections were bleached in 70 % alcohol and the number of vascular bundles were counted under a binocular microscope. Segregants with extremely few bundles (negative selection) and very many bundles (positive selection) were allowed to recover and produce seed. Seed harvests from

Table 4. Larval attack by *Oscinella frit* in relation to plant base diameter and density of vascular bundles in 8 oat cultivars 22 days after sowing.

Cultivar	% larval attack ¹⁾	Plant base diameter (mm) ²⁾	No. of vascular bundles ³⁾
Hede	71	3.20	13.0
Spet	66	3.17	15.4
Selma	61	3.13	15.8
Summer	61	2.50	16.6
Sörbo	50	3.02	18.1
Victory	47	3.21	18.8
Sang	42	3.05	18.4
Gotland	36	3.24	18.2

1) Data from IV.

- 2) Plant base diameters were determined just above the coleoptile apex. The mean values given are based on measurements of 10 plants per cultivar (unpubl. data).
- 3) The vascular bundles refer to the longitudinal sclerenchymatous structures visible between the 7 normal leaf veins of the leaf sheath of the first leaf. The mean values given are based on countings on 10 plants per cultivar (unpubl. data).

individual selected plants were kept separate in the subsequent F_3 -test. Here, 10 plants were used for anatomical studies as described above. An additional 35 F_3 -plants from each of the F_2 -selections were used in a biological test. Each plant was provided with two frit fly eggs. After 3-4 weeks all plants were dissected and symptoms of attack and numbers of pupae were recorded. There was no significant difference in frequencies of unattacked (resistant) plants in positive and negative selections (24 and 18 %, respectively). Significant effects of the selection was observed, however, both regarding the anatomical character (20 % more vascular bundles in positive selections) and the survival of frit fly larvae (22 % fewer pupae in positive selections). The data are shown in Tab. 5. The analysis of variance (Tab. 6) demonstrated that there were significant differences among plants within selections, which indicates that segregation still occurs and that a procedure of further selection would probably increase the difference between the two sub-populations.

Table 5. The effect of positive and negative selections of vascular bundle density in a F_2 -population of the cross (Gotland x Sang) x Sv 80384 tested in 11 + 11 individual plant progenies (F_3 -plants).

Mean no. of vascular bundles		Mean no. of pupae/35 plants	
Pos. sel.	Neg. sel.	Pos. sel.	Neg. sel.
10.8	7.7	26	27
12.4	8.4	16	37
9.0	7.2	31	30
10.2	9.5	18	26
8.6	8.3	17	23
10.2	5.8	26	32
11.7	8.2	24	33
6.6	8.0	18	20
7.8	9.8	20	33
9.6	9.3	26	24
11.6	8.2	16	22
$\bar{x}$ 9.9	8.2	21.6	27.9

Table 6. Nested ANOVAs on data from Tab. 5. A) Numbers of vascular bundles in 220 F_3 -plants representing 11 positive and 11 negative selections from a segregating F_2 -population. B) Numbers of frit fly pupae per replicate in a test with a total of 770 F_3 -plants representing the same 11 + 11 selections as in A. Five replicates with 7 plants each were used in all selections.

A)				
Source of variation	d.f.	MS	F	P
Among selections (pos. vs. neg.)	1	148.91	6.80	< 0.05
Among plants within selections	20	21.90	2.31	< 0.001
Within plants	198	9.47		
B)				
Among selections (pos. vs. neg.)	1	43.28	7.71	< 0.05
Among plants within selections	20	5.61	1.81	< 0.05
Within plants	88	3.10		

C) INTERACTION BETWEEN RESISTANCE TO OVIPOSITION AND RESISTANCE TO LARVAL PENETRATION

Lupton (1981) concluded with reference to a study by Bingham and Lupton (1958) that differences in frit fly resistance in oats are difficult to demonstrate and irregular in their expression. The irregularities may be caused by the complicated interaction between A) resistance to oviposition and B) resistance to larval penetration.

Field and greenhouse experiments indicate that resistance to oviposition and resistance to larval penetration act at different stages of the oat plant development (V). There were significant differences in oviposition attractivity among cultivars when the plants were very young (one- to two-leaf stage). One week later (two- to three-leaf stage) no differences in oviposition attractivity could be detected. Resistance to larval penetration worked in the opposite way: Young plants were equally susceptible but in the later stage of development there were significant differences among the cultivars studied (Fig. 5).

Consequently, if plants are attacked early, cultivars susceptible to oviposition suffer the greatest damage. However, if the frit fly invasion occurs later, cultivars susceptible to larval penetration suffer the greatest damage. These effects were confirmed in a cage experiment in the field, where different oat cultivars were exposed to frit fly attack at different developmental stages (V). Fig. 5 shows that cv. Gotland is susceptible to oviposition at an early stage of development. At a later stage, the same cultivar appears to be fairly resistant to larval penetration. Cvs Summer and Selma seem to react the opposite way. In a study of eight oat cultivars (IV), there was an inverse relationship between resistance to larval penetration and resistance to oviposition. Such a negative relationship means that a cultivar may show different levels of resistance in different field experiments depending on the stage of plant development at the time of frit fly attack. A series of field experiments similarly showed that oat cultivars which appeared to be susceptible to frit fly damage at a late sowing date turned out to be relatively resistant when sown early - and vice versa.

The complicated interaction between resistance to oviposition and resistance to larval penetration certainly produces difficulties when field experiments are to be evaluated. Sometimes resistance to oviposition has a dominating influence and sometimes resistance to larval penetration is the most important factor. In late sown experiments, where the frit fly inva-

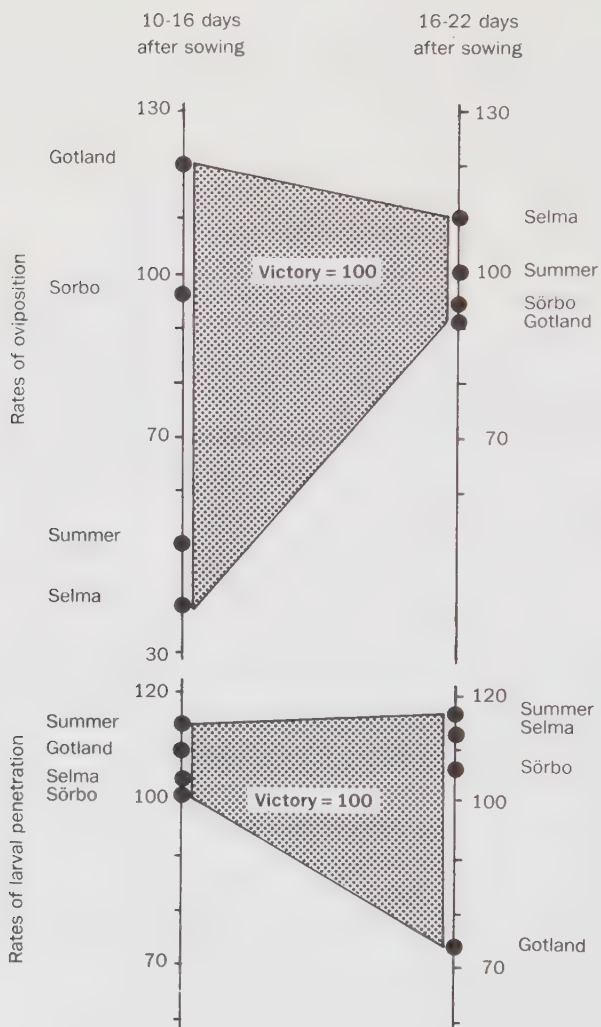


Figure 5. Relative rates of oviposition and larval penetration in different oat cultivars at two growth stages (from V).

sion starts at an early developmental stage of the plants, resistance to oviposition tends to dominate the final expression of resistance. In early sown experiments on the other hand, where frit fly attack starts when the plants are older, resistance to larval penetration is more important.

In most studies on frit fly resistance, late sowing has been practised to establish a sufficiently high level of attack. As a result the oviposition component of resistance has often become exaggerated. This implies that an evaluation of frit fly resistance in late sown field experiments may be doubtful, since a high level of susceptibility to oviposition may result in a heavy attack in an early developmental stage. A heavy attack of that kind may mask a desirable resistance to larval penetration in later stages. This is a fatal effect, since the oat crops of southern Sweden normally are sown early enough to escape very early attacks by Oscinella. When damage occurs, it is in most cases caused by larvae invading the plants at a stage when resistance to larval penetration starts to develop. From a practical point of view early resistance to larval penetration therefore seems to be better than a certain degree of resistance to oviposition. Consequently, mechanisms conferring a high degree of resistance to larval penetration should be given priority in a frit fly resistance breeding programme in oats.

IS IT POSSIBLE TO BREED OATS FOR FRIT FLY RESISTANCE?

The idea of breeding oats for frit fly resistance is as old as modern plant breeding itself. Nilsson-Ehle (1906) reported varietal differences in frit fly attack and later Åkerman contributed with interesting data from a long series of field trials. The data and material collected by Nilsson-Ehle and Åkerman were presented to Cunliffe, who visited the Swedish Seed Association, Svalöf, in 1927 (Cunliffe 1929). After a thorough study on the resistance of many different genotypes of oats Cunliffe published the results in a series of papers 1929 - 46. The highest levels of frit fly resistance were found in certain lines derived from old Scandinavian land varieties, e.g. Summer (from Gotland), Spet (from Småland), and Hede (from Denmark). These lines were also included in my own studies (III-V). Early attempts were made to combine the frit fly resistance of these lines with a better yielding capacity from other sources (Cunliffe 1936, Cunliffe and Hodges 1946). Unfortunately no agronomically acceptable lines resulted from these crosses. Better practical results were obtained with crosses including von Lochow's yellow oats, a drought tolerant and moderately frit fly resistant German cultivar (Åkerman 1951).

Complete frit fly resistance has never been reported from any investigation in Avena. Even the most resistant lines obtained so far may be heavily attacked if sown late in the spring. Resistance to frit fly attack therefore appears to be a relative concept.

Some opportunistic traits, especially the wide host plant range, indicate a broad ecological amplitude in O. frit. Therefore it may be assumed that the fly has a good ability to withstand many possible defence strategies of the host plants. It seems unlikely that e.g. minor modifications of specific chemical substances in oats could be used as a means of improving frit fly resistance. The wide host plant range of the parasite suggests that some general "grass chemicals" are involved in the host plant recognition. Consequently it seems unrealistic to believe that oats could be chemically manipulated through plant breeding in such a way that the frit fly would not recognise the plants as potential hosts. This argument leads to a rather pessimistic view on the possibilities of breeding oats for resistance to frit fly attack. Host plant resistance is not merely a question of chemistry however, and if we consider the possibility of utilizing non-specific structural defence mechanisms in the young oat plant, there is every prospect of developing a successful plant breeding programme.

The stereotyped oviposition behaviour of the frit fly may be a weak point, which makes the fly vulnerable to certain morphological adaptations in the host plant. Fig. 2 shows that the frit fly is "squeezed" between two opposing selection forces to lay eggs on oat seedlings around the two-leaf stage. This stage coincides with the coleoptile separation phase. If the coleoptile separation could be delayed, the fly would have to lay her eggs later. This would result in an increased larval mortality due to the increasing resistance of the host plant to penetration. Similarly, if the production of sclerenchymatous vascular bundles in the leaf sheaths could be induced earlier in the seedling development, larval mortality would increase. Theoretically, therefore, the plant breeder's aim should be to select an oat plant ideotype that in the seedling stage allocates a maximum of resources to build up the sclerenchymatous bundles of the main shoot as early as possible. Ideally, this anatomical character should be combined with a late coleoptile separation, which prevents oviposition until the resistance to larval penetration is well developed.

BREEDING METHODS

It is possible that the mechanisms of resistance to larval penetration are based on several factors - both structural and chemical. Shapiro et al. (1959) regarded a rapid lignification in maize seedlings as an important factor in resistance to frit fly attack. Moore (1984) showed that a high content of silica in tillers of Italian ryegrass enhanced resistance to penetration by frit fly larvae. Although based on a small range of material, the strong negative correlation between the number of vascular bundles and larval attack (Tab. 4) and the positive selection effect obtained in the segregating oat population (Tab. 5) are both encouraging results. If a causal relationship exists, the density of vascular bundles of the first leaf sheath - an easily observed character - could be used as a guide when searching for segregants with better resistance to penetration by frit fly larvae. Similarly, the desirable coleoptile character would be very simple to select for, even in a larger scale breeding programme.

Although selection for frit fly resistance may be accomplished by screening the breeding material for desirable morphological and anatomical plant characters, biological tests have to be made as well. The time-consuming and expensive biological tests may be restricted, however, to the most advanced breeding generations. The biological tests should preferably be carried out under authentic field conditions. This desire for authenticity may create problems however, since early sowing often results in low levels of attack, which gives an unreliable estimate of the levels of resistance. Late sowing, on the other hand, will be unfavourable to genotypes resistant to larval penetration and susceptible to oviposition. The problem can be solved if late sowing is practised and the assessment of the frit fly attack is made twice during the early plant development. The first assessment is made as soon as the symptoms of main shoot attack are clearly visible. This gives an estimate of differences among genotypes with regard to oviposition susceptibility. A second assessment of the material is then made about one week later. The difference in proportions of attacked main shoots between the second assessment (early + late damage) and the first (early damage) will give an estimate of how rapidly the resistance to larval penetration develops. Tab. 7 shows examples from two field trials, where such a double assessment has been practised.

The results in Tab. 7 show that cv. Gotland develops resistance early, while cv. Selma is susceptible to attack for a longer period. These results are consistent with previous greenhouse (IV) and field (V) experiments and are also in accordance with the results shown in Fig. 5.

Table 7. Proportions (%) of main shoots attacked by frit fly in five oat cultivars in two late sown field experiments. The figures given are mean values based on 4 replicates. The frit fly attack was assessed twice with an interval of a week (unpubl. data).

Cultivar	Experiment 1			Experiment 2			Mean difference experiments 1 and 2
	Assessment		diff. 2-1	Assessment		diff. 2-1	
	1	2		1	2		
Selma	28.5	48.5	20.0	49.3	58.3	9.0	14.5
Victory	22.8	38.0	15.2	49.0	53.0	4.0	9.6
Summer	5.3	13.3	8.0	21.0	24.8	3.8	5.9
Sörbo	10.8	11.8	1.0	46.8	49.5	2.7	1.9
Gotland	29.8	32.0	2.2	47.5	47.5	0.0	1.1

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Frit fly *Oscinella frit* oviposition on oat seedlings: ecological significance of the host plant selection

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Jonasson, T. 1977. Frit fly *Oscinella frit* oviposition on oat seedlings: ecological significance of the host plant selection. – Oikos 29: 104–111.

The oviposition behaviour of *Oscinella frit* L. was studied in a series of greenhouse experiments. The crevice between the coleoptile and the plant base in oat seedlings was strongly preferred by the frit fly female as oviposition site. A simultaneous reception in the female of (a) a tactile stimulus from the coleoptile crevice or a soil crack and (b) a chemical stimulus from the plant appeared essential for a high oviposition rate. The oat plants were maximally susceptible to oviposition around the two-leaf stage, when the coleoptiles as a rule were disconnected from the plant bases but not yet wilted.

Three selective advantages associated with oviposition behind the coleoptile of oat seedlings in the two-leaf stage may be pointed out: (1) Frit fly larvae hatching on oat plants in the two-leaf stage have achieved an optimal compromise between the risk of not being able to penetrate too old a host plant and that of starvation on too small a plant, (2) larvae hatching near the base of the plant have the shortest way to penetrate before they reach the meristematic region, where the feeding takes place, and (3) eggs placed behind the coleoptile are protected against predators.

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Исследовали поведение при яйцекладке *Oscinella frit* L. в серии опытов в вегетационных домиках. Щель между coleoptile и основанием растения в проростках овса предпочитаемое место для яйцекладки. Одновременный прием самками а) тактильного стимула от щели coleoptile или трещины в почве и б) химического стимула от растения имеют большое значение для ускорения яйцекладки. Проростки овса особенно удобны для откладки яиц на стадии второго листа, когда coleoptile, как правило, не связано с основанием растения, но не сразу увядает.

Установлены три фактора, определяющие преимущество откладки яиц позади coleoptile на стадии второго листа: 1 – личинки мух, выходящие на стадии второго листа, достигают оптимального компромисса между риском не проникнуть внутрь более взрослого растения и опасностью голодания в слишком молодых растениях. 2 – личинки, вышедшие у основания растений, проникают в меристемную ткань по кратчайшему пути, где они и питаются и 3 – яйца, отложенные позади coleoptile, защищены от хищников.

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1. Introduction

The frit fly *Oscinella frit* L. is a very common species of grasslands in southern Sweden and is also a pest of cereals. In regions where late spring sowing often is unavoidable, the larvae sometimes cause severe damage to oats, feeding in the young shoots.

A possibility of breeding oats for a higher degree of frit fly resistance has been indicated repeatedly by marked varietal differences in susceptibility to attack in the field. According to Cunliffe and Hodges (1946), Bingham and Lupton (1958) and Peregrine and Catling (1967), such differences are due to different rates of oviposition on different cultivars, i.e. frit fly resistance seems to be associated with non-preference for oviposition.

Investigations have previously been made to analyse the egg-laying behaviour of *O. frit* and to elucidate the sequence of stimuli required to release oviposition. Riggert (1935), Andersson (1956) and Sanders (1960) all emphasized the preference of the female to lay eggs behind the disconnected coleoptile of the oat seedling. Ibbotson (1960) concluded that two groups of stimuli were necessary for egg-laying to occur. The first component (probably biochemical) originated from the plant itself, and the second was a proprioceptive component resulting from the disposition of legs and ovipositor of the female and was not dependant on the presence of a host plant.

The present study analyses experimentally the oviposition behaviour of the frit fly with special reference to the ecological significance of the host plant selection.

2. Material and general methods

Oat plants (cv. Victory) were cultivated in peat soil in 25 cm plastic buckets or 8 cm plastic pots. Transparent plastic cylinders with nylon net tops were used as insect cages during the oviposition period. The frit flies were obtained from a culture established with specimens collected from infested oat panicles and maintained in the greenhouse at 20–22°C, 16 h light period. Under these conditions the generation time was about 30 d. The adult flies were fed with a mixture of water, sucrose, and powdered milk (Le Berre et al. 1961).

In experiments with several flies and many plants within the same cage, newly emerged adults in a sex

ratio about 1:1 were used. The flies were sexed according to body size, males being smaller than females. Unless otherwise stated, only females in the reproductive phase were used in the other experiments. Eggs used in egg transfer experiments were less than two days old when collected from the breeding cages and carried over to the test plants with a moistened brush.

The first part of a germinating oat seed to emerge above soil surface is the coleoptile. From inside this parenchymatous closed tube the first leaf of the plant develops. The apical part of the coleoptile is broken through and the remnants form a tight fitting sheath around the plant base. The coleoptile is, however, an ephemeral structure which soon loses its firmness and begins to disconnect from the plant. The apex is bent outwards, and a gradually expanding crevice along the plant base is formed until, finally, the coleoptile is totally wilted.

Plants in various developmental stages were used in the experiments. Normally the seedlings began to emerge 4–5 d after sowing. The developmental stages and the corresponding coleoptile appearances of different plant ages under the prevailing greenhouse conditions are indicated in Tab. 1.

Only eggs deposited behind coleoptiles ("coleoptile eggs") were recorded in the first experiment. In all other egg-laying experiments eggs laid in the soil ("soil eggs") were also taken into account.

3. Procedure and results

3.1. Effect of plant age on oviposition sites and larval attack

Procedure

Frit fly oviposition and subsequent larval attack in relation to plant age were studied in an experiment with four different developmental stages of plants. Four replicates per plant age were used, and each replicate consisted of 20 flies and about 50 plants. The flies were introduced in the cages 6, 10, 16, and 22 d after sowing, respectively, and the plants were exposed to oviposition for six days.

Results

No spontaneous tillering occurred during the oviposition period, so practically all eggs were laid either be-

Tab. 1. Age-specific developmental stages and coleoptile conditions in oat plants (cv. Victory) cultivated in a greenhouse at 20–22°C, 16 h light period.

No. of days after sowing	Developmental stage	Coleoptile condition
5	First leaf just emerging	Col. closely affixed to the plant base
9	Second leaf emerging	Col. beginning to disconnect
15	Two leaves fully developed	Col. disconnected from the plant base
21	Three leaves fully developed	Col. beginning to wilt
27	Fifth leaf developing	Col. wilted

Tab. 2. Rates of oviposition behind the coleoptile and main shoot damage in relation to plant age. Means within each column followed by different letters differ significantly at the 5% level according to the Student – Newman – Keuls test (Sokal and Rohlf 1969).

Plant age (days after sowing) when flies were introduced	Mean proportion (%) of plants	
	with eggs behind the coleoptile	with larval damage to the main shoot
6	1.5 a	89.5 a
10	16.5 b	92.4 a
16	73.2 c	85.8 a
22	60.7 d	20.1 b

hind the coleoptiles or in cracks between the plant bases and the soil surface. These cracks were available throughout the experiment and were presumably not affected by the plant development. Consequently, the increasing frequency of coleoptile eggs in concordance with the increasing frequency of coleoptile disconnections indicates a preference of the frit fly for laying eggs in the coleoptile crevice. The maximum proportion of plants with coleoptile eggs occurred before the coleoptiles began to wilt (Tab. 2).

According to the proportions of plants with main shoot attack, it is evident that soil oviposition was frequent in the cages, at least in those containing young plants. It is also obvious that the oldest plants had become resistant to larval attack.

3.2. Egg-laying rate in relation to coleoptile condition

Procedure

Oat seedlings in the early two-leaf stage were used. In one series the coleoptiles were artificially separated from the plant bases. In the other they were left intact, i.e. closely attached to the stems. Each replicate was composed by one mated female and one single plant caged together for three days.

Results

In the series with separated coleoptiles the mean number of eggs (coleoptile eggs + soil eggs) laid per ovipositing female was 10.1 (S.E. = ± 0.87 ; range: 1–15; $n = 17$). In the other series the mean number was 6.0 (S.E. = ± 1.00 ; range: 1–14; $n = 16$). The difference between the two means was significant ($t = 3.06$; $P < 0.01$).

Although the flies were able to deposit their eggs in the soil, plant with closely attached coleoptiles received fewer eggs than plants with disconnected coleoptiles. This may explain why the maximum proportion of attacked main shoots in the previous experiment did not occur in the cages with the youngest plants (Tab. 2).

3.3. Oviposition behaviour

The preference of the female to deposit her eggs behind the coleoptile was demonstrated by a very characteri-

stic behaviour. Often walking in a spiral around the plant base, with the extended ovipositor trailing on the surface, the female investigated the coleoptile region in great detail. Surface irregularities made her stop walking and, instead, she began to alternately protract and retract the ovipositor along the edges of the protruding structure. This behaviour eventually made it possible for the fly to insert the ovipositor in a suitable crevice and lay an egg. The apical part of the coleoptile, which was more or less projecting from the plant base (depending on the degree of disconnection), appeared to be the main subject for these penetration attempts. Plants without a suitable crevice behind the coleoptile were either abandoned or – usually after many abortive attempts – provided with an egg in the interspace between plant base and soil surface.

3.4. The localization of egg-laying sites: searching time and number of investigated plants

Procedure

Newly emerged flies were randomly divided into two groups. One group was confined to young oat plants with few coleoptiles disconnected. The other was isolated with older plants which had many coleoptiles disconnected. After 2–3 d, when ovipositions became frequent, the procedure of egg-laying was studied in detail. The observations started when a female was seen walking on a plant with the ovipositor extended. The female was then followed and its pre-oviposition movements were recorded. Every plant entered by the fly was recorded as a new one, even if it had already been investigated by the same fly.

Results

The localization of a suitable egg-laying site was a time-consuming task for the females. In the cages with young plants, where the probability of finding a plant with disconnected coleoptile was low, many abortive attempts at oviposition occurred before the egg finally was laid, in most instances in the soil (Tab. 3). Although the searching time may seem long, it only includes the time of active searching immediately before the oviposition. The total interval between two consecutive ovipositions is probably much longer, including e.g. feeding and cleaning activities as well as periods of inactivity.

All observed females completed the sequence of searching movements by depositing one single egg. When the egg was laid, the flies usually flew away and landed on the roof of the cage.

3.5. Consequences of delayed oviposition

Procedure

Another batch of newly emerged flies were randomly divided into two groups, which were confined to young and old plants, respectively. After six days forty females from each group were taken for further studies.

Tab. 3. Searching time and number of investigated plants before oviposition in two groups of frit fly females confined to young and old oat seedlings, respectively. The probability values were obtained using t-tests and Fisher's exact test for independence (Sokal and Rohlf 1969).

Plant condition	No. of obs. ♀♀	Searching time (min) before the egg was laid		No. of plants investigated before the egg was laid		Proportion of eggs laid behind coleoptiles (%)
		Mean ± S.E.	Range	Mean ± S.E.	Range	
Young plants; few coleoptiles disconnected	20	8.3 ± 1.45	1.2 – 28.2	3.8 ± 0.70	1 – 12	20
Old plants; many coleoptiles disconnected	20	3.2 ± 0.37	1.1 – 6.8	1.2 ± 0.12	1 – 3	75
Test of significance		t = 3.44; P < 0.01		t = 3.67; P < 0.001		P = 0.001

Twenty flies of each category were dissected and examined for mature eggs. The remaining specimens were used in an egg-laying experiment, where each female was kept isolated with one oat plant until death.

Results

Among the flies previously isolated with young plants 13 contained mature eggs (65%). In the other group 6 females had mature eggs in their ovaries (30%). According to Fisher's exact test for independence (Sokal and Rohlf 1969), the difference was nearly significant (P = 0.056). Similar results were obtained in the egg-laying experiment. Among the flies previously confined to young plants 17 egg-laying specimens occurred (85%). In the other group only five were able to lay eggs (25%). Here, the difference was highly significant (P = 0.0003).

As fecundity presumably did not differ between the two groups of flies, and since oviposition started in both groups during the introductory confinement, the results indicate that the flies that were isolated with suitable host plants rapidly laid their eggs and then passed into the postreproductive phase. The flies that were isolated with poor oviposition targets, however, retained their eggs in the ovaries. When easily accessible oviposition sites later appeared, these eggs could readily be laid.

3.6. Releasing oviposition stimuli

Procedure

The oviposition behaviour of *O. frit* proves that a narrow crevice plays an important role in the selection of egg-laying sites. Egg-laying in just any narrow slit does, however, obviously not occur. In an experiment with four different artificial oviposition targets the possible interaction of the stimuli emanating from a crevice and an oat leaf, respectively, was tested. The design of the plant models was as follows:

- A. A coleoptile dummy + a real oat leaf
- B. A coleoptile dummy + a green leaf-shaped plastic strip
- C. A real oat leaf only
- D. A green leaf-shaped plastic strip only

The coleoptile dummies were made of 3–4 cm sections

of green plastic straws. The ends were cut off obliquely, and the sections were pressed down into the soil leaving 5–10 mm above the surface. The oat leaf or plastic strip was then fitted into the upper end of the straw. Models without coleoptile dummies were suspended in thin threads from top of the cage. In this way contact with the soil surface was avoided. The four models were presented to 25 flies for 24 h in 17 replicates.

Results

The results given in Table 4 indicate that the stimuli emanating from a crevice and an oat leaf must act together to release oviposition.

On the most effective plant models (designated as "A" above) the eggs were laid around the edge inside the coleoptile dummy, where the oat leaf was attached. No eggs were laid in the soil, which may indicate that the spatial separation of the "oat-leaf stimulus" and the "soil-crevice stimulus" by 5 to 10 mm was enough to prevent oviposition. To test this hypothesis an experiment with semi-artificial plants (model "A" above) was performed.

In one series the coleoptile dummies were treated with oat leaf juice, and in a control series the dummies were treated with pure water. One semi-artificial plant and one mated female were used in each replicate.

Tab. 4. Top: Mean number of frit fly eggs laid in a free choice experiment with four different artificial oviposition targets. Bottom: An analysis of variance on square root transformed data.

	Oat leaf	Plastic strip		
With coleoptile dummy.....	8.5	0.2		
Without col. dummy	0.2	0.0		
Source of variation	df	MS	F	P
Oat leaf/Plastic strip	1	14.97	22.68	<0.001
With/Without col. dummy	1	14.31	21.68	<0.001
Interaction	1	11.64	17.64	<0.001
Error.....	64	0.66		

Tab. 5. Results from an experiment with different developmental stages of oat plants, all artificially provided with one frit fly egg.

Egg transfer, no. of days after sowing	No. of eggs and plants (n)	Proportion of larvae (%) [*] penetrating main shoot	Proportion of penetrating larvae (%) staying inside the main shoot	Proportion of surviving larvae (%) [*] (incl. migrants)
5	59	72	15	33
9	59	72	42	43
15	52	62	88	57
21	55	23	100	23
27	51	0	—	0

^{*} Figures adjusted according to a 78% hatching rate.

Out of 19 “plants” with eggs in each series, 8 with leaf juice treated coleoptile dummies got eggs in the soil. In the control series only one was provided with soil eggs. According to Fisher’s exact test, the difference was significant ($P = 0.019$). Thus the result support the hypothesis that two types of stimuli (tactile and chemical) must act simultaneously on the female to elicit oviposition.

3.7. Age specific host plant properties: quality versus quantity *Procedure*

Young oat plants are more susceptible to penetration by frit fly larvae than old plants. An extremely young oat plant would be easy to pierce but, on the other hand, it would also provide a very limited supply of food. Thus, a larva attacking an extremely young plant would run a risk of exhausting the available resources. In an experiment with different developmental stages of oat plants,

each being artificially provided with one frit fly egg, the interrelations of the larva and its host was examined. The test plants were inoculated with eggs 5, 9, 15, 21, and 27 d after sowing, respectively. For a hatching rate check, sixty eggs were placed on moist filter paper in Petri dishes. Two weeks after the egg transfer the plants were dissected and examined for symptoms of larval attack, and the remaining larvae and pupae were collected. If not only the main shoot, but also the tillers were attacked, the larva was considered a migrant. The tillers always developed after the main shoot was penetrated.

Results

The youngest plants were very susceptible to larval attack but the ability of the main shoot to support the larvae (expressed as the proportion of non-migrating individuals) was low. Older plants, in contrast, were more resistant to penetration attempts but among the successful larvae few left the main shoot (Tab. 5). The

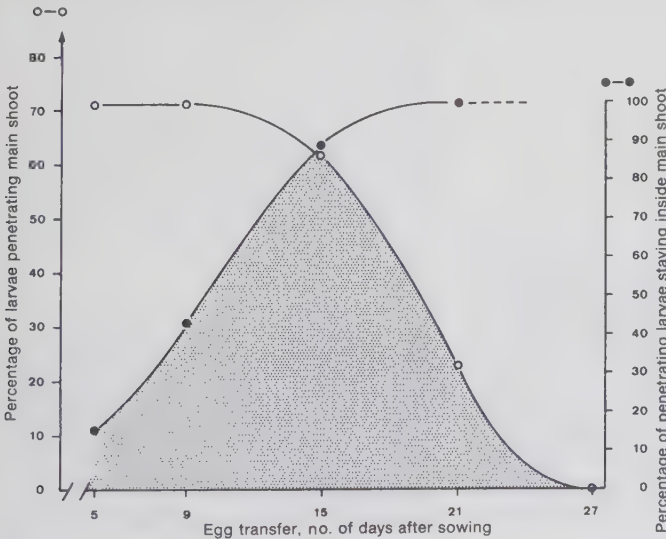


Fig. 1. The ability of newly hatched frit fly larvae to penetrate the main shoots and the ability of the main shoots to support the growing larvae in relation to plant age (data from Tab. 5).

Tab. 6. *Top*: Number of larvae/plant (mean $\pm$ S.E.) in a combined greenhouse/field experiment with frit fly eggs artificially added to the plants. *Bottom*: An analysis of variance on the obtained data.

Degree of plant exposure		Col. eggs	Soil eggs
Field series, exposed plants		2.76 $\pm$ 0.240	1.52 $\pm$ 0.209
Field series, protected plants		2.52 $\pm$ 0.265	2.00 $\pm$ 0.208
Greenhouse series		2.16 $\pm$ 0.189	2.20 $\pm$ 0.163

Source of variation	df	MS	F	P
Coleoptile/Soil eggs	1	12.326	10.663	<0.01
Degree of plant exposure	2	0.187	0.162	>0.75
Interaction	2	5.147	4.452	<0.05
Error	144	1.156		

intersection of the graphs in Fig. 1, which coincides with the two-leaf stage, indicates optimal conditions for the frit fly larvae. In fact, even if migration is left out of consideration, the highest rate of survival was obtained among larvae hatching on plants in that stage (Tab. 5).

3.8. Host plant invading capacity by larvae in the field

Procedure

In a combined greenhouse/field experiment with different degrees of exposure of coleoptile and soil eggs, respectively, the host plant invading capacity of the newly hatched larvae was studied.

Oat plants in the two-leaf stage, grown singly in small plastic pots, were artificially provided with four frit fly eggs each. Assuming an egg-hatching rate of 78% and a 62% penetration success (Tab. 5), these four eggs would theoretically yield two penetrating larvae, which seems to be an amount low enough to prevent severe competition within the host plant.

Eight series with 25 plants each were prepared for the experiment:

- A. In three series the eggs were placed behind the coleoptile
- B. In three series the eggs were placed in the soil, quite close to the plant base
- C. In two series no eggs were added (control series)

One series of (A) and (B) were left in the greenhouse, and the remaining ones were placed in a 150 m² field plot with young oats. One series of (A), (B), and (C) were put into wider pots buried in the ground. In this way a pit-fall trap effect was attained, preventing ground living predators from reaching the eggs ("Protected plants"). One series of (A), (B), and (C), finally, were buried in the ground, so that ground living predators could freely pass across the pot soil surface ("Exposed plants"). The pots were arranged in a block design, with the six different kinds of test plants randomized within each of the 25 blocks. The distance between the pots was 50–75 cm. After 7 d in the field the pots were collected and brought back to the greenhouse. A week later all plants were dissected and examined for larvae.

Results

In the control series from the field the mean number of larvae/plant in protected and exposed plants was 0.60 (S.E. = $\pm$ 0.173) and 0.76 (S.E. = 0.156), respectively. These figures give an estimate of the natural infestation rate during the experiment. The difference between the two means was not statistically significant ($t = 0.687$; $P > 0.5$). In Tab. 6 the results obtained from the series with artificially added eggs are given. An analysis of variance including all series proves that there was a significant difference in host plant invading capacity of larvae hatching from coleoptile eggs and soil eggs, respectively. There was no statistical significance between different levels of exposure, but the significant interaction between egg deposition site and plant exposure suggests that different levels of exposure to ground living predators affected coleoptile eggs and soil eggs unequally. In the protected environment of the greenhouse, larvae hatching from soil eggs and coleoptile eggs had the same capability to survive and reach the host plant. In the field, however, soil egg larvae to a considerable extent failed to invade the host plant, at least when the test pots were fully exposed to predators. Among the predacious beetles collected in the pit-fall traps surrounding the protected plants were i.a. the carabids *Agonum dorsale* Pont., *Bembidion lampros* Hbst. and *Trechus quadristriatus* Schr., all reported by Jones (1969) to feed on frit fly larvae.

4. Discussion

Cunliffe et al. (1925) exposed oat plants of different stages of growth to a natural frit fly population and found that the probability of the main shoots being attacked was maximal during the two- and three-leaf stages. "Plants in the early one-leaf stage", they concluded, "showed a certain degree of immunity, due probably to size non-attractiveness." According to my experiments, *O. frit* presented a strong preference for ovipositing in the coleoptile crevice. The proportion of plants with eggs behind the coleoptile reached a maximum

somewhere between the early two-leaf stage and the late three-leaf stage (Tab. 2).

Quality and quantity of the host plant are two conflicting properties which determine the probability of survival of the frit fly larvae. From the egg an agile larva hatches, which burrows into the oat shoot and enters the meristematic region. After a certain age the plant is impossible to penetrate, while, on the other hand, a very young plant offers an insufficient supply of food. According to the greenhouse results, larvae hatching on plants in the two-leaf stage had achieved an optimal compromise between the risk of not being able to penetrate the host plant and the risk of over-exploiting it. Therefore, to maximize her fitness, the frit fly female should lay her eggs on plants in that stage, which, interestingly enough, seems to coincide fairly well with the coleoptile disconnection phase.

Riggert (1935) and Jones (1969) reported from their experiments that over 90% of the frit fly eggs were laid behind coleoptiles, and Jepson and Southwood (1958) considered soil oviposition in the field to be very rare. Soil cracks at the plant bases were indeed frequently utilized as egg-laying sites by the flies in the greenhouse cages, especially when coleoptile oviposition failed, but compared with the situation at the coleoptile, the stimulation for oviposition appeared to be weaker at the soil level.

Since, according to my field experiment, predation on frit fly eggs and (or) first instar larvae in the soil seemed to be an important mortality factor, oviposition at predator protected sites certainly would be selected for. Compared with other possible hiding-places for the eggs on a young oat plant, the selective advantage associated with oviposition behind the coleoptile is emphasized by the fact that larvae hatching near the base of the plant have the shortest way to penetrate before they reach the meristematic region, where the feeding takes place.

The coleoptile condition, which seems to be a crucial point for the oviposition attractiveness of a host plant, is an inconspicuous character. Presumably the frit flies are capable of discriminating between different developmental stages of the larval host plants without a close examination of each specimen. Visual stimuli may be involved in the recognition of a specific stage, since not only colour, but, according to Sanders (1960), also shape and size of the plant affected the orientation of flight in *O. frit*. Although such a capability of a primary sorting of the potential host plants may exist, the laying of eggs is a time- and energy-consuming activity for the females. The eggs are laid one by one, and each oviposition is preceded by a lengthy procedure of selection of a suitable egg-laying site. Therefore the frit fly is able to lay only a small number of eggs. Rygg (1966) reported a total mean production of about forty eggs per female under laboratory conditions.

The oviposition is an act of extreme importance to the frit fly female. Failure to lay her eggs at sites where they and the larvae have a reasonable chance of surviving

will lower her fitness drastically. It is therefore not surprising that a whole sequence of environmental criteria are involved in her selection of egg-laying sites. Key oviposition stimuli from the host plant seem to be a prerequisite for egg-laying to occur. Ibbotson (1960) found that frit flies isolated from host plants failed to lay eggs over a long period, although carrying mature eggs in their ovaries. Similarly, according to Hillyer (1965), the weak host plant stimulation from *Dactylis*, which is considered highly resistant to frit fly attack, led to a retardation of egg production. My experiments with flies confined to very young plants correspondingly indicated that the oviposition rate was low and that eggs were retained when few suitable egg-laying sites were available.

My conclusion agrees with that of Ibbotson (1960) that two groups of stimuli are necessary to release oviposition in *O. frit*. Ibbotson, however, considered the soil around the plant, not the coleoptile, to be the main source of tactile stimulation in connection with frit fly oviposition. According to my results, it seems reasonable to suggest that the tactile stimulus from a narrow crevice, particularly the coleoptile crevice, constitutes a very important part of the total stimulus pattern. The other main component would be a chemical stimulus. Continual tasting movements with the protracted proboscis during the searching for egg-laying sites are a conspicuous element of the oviposition behaviour of the frit fly, and gustation is most likely involved. Contact chemoreception also explains why the two groups of stimuli could not be spatially separated and yet elicit oviposition.

A close connection between the different components of the total stimulus pattern obviously enhances the survival of frit fly progeny. If an almost simultaneous reception in the female of the tactile and the chemical stimuli is required to release oviposition, she will be prevented from laying her eggs on the smooth surface of leaves and straw, where the eggs might easily be dislodged by a rain shower. Nor will she straggle too far away from the plant and hence have to oviposit in the soil, where the eggs or the larvae may be detected by predators.

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SHORT COMMUNICATION

Thomas JONASSON¹⁾: *Frit fly (Oscinella frit) oviposition on oat seedlings: evidence for contagious distribution of eggs*

KEY WORDS: *Oscinella frit* — Diptera — Chlo-
ropidae — Oviposition behaviour — Egg dis-
tribution — Host-plant selection

Host-plant selection and oviposition in *Oscinella frit* are probably guided by an intricate pattern of stimuli (Ibbotson, 1960; Sanders, 1960; Jonasson, 1977). The egg-laying behaviour is extremely stereotyped and most eggs laid on oat seedlings are deposited behind the loose coleoptile. The frit fly ♀ normally lays only one egg at a time; after depositing the egg she usually moves away to enter another plant (Jonasson, 1977).

Multiple ovipositions on the same plant have been reported by Andersson (1956) and Jones (1969), but very little is known about the consequences of this phenomenon. Considering the limited food supply provided by a young plant, multiple oviposition seems to be a wasteful strategy for the frit fly ♀. The distribution of frit fly eggs with special reference to the ecological significance of multiple ovipositions has been studied here.

Materials and methods — Field observations on egg distribution pattern were done on 200 seedlings in a late sown 10 m² oat plot situated on the edge of a large field of early sown oats.

The experiments were performed in a greenhouse at 20—22° and 16 hr light period. Flies for oviposition experiments and eggs for the inoculation experiments were obtained from a culture maintained in the greenhouse for less than 5 generations. The oat plants were cultivated in a standard peat soil mixture in 25 cm plastic buckets or 8 cm plastic pots.

In 2 experiments oat plant dummies with a "coleoptile" and a "leaf" component were used instead of real oat plants. The "coleoptile" component was made of a 3—4 cm section of a green plastic drinking straw (diam 3 mm) which was cut off at an angle of about 45° pressed down into the soil leaving 5—10 mm above the surface. The "leaf" component was a 4 × 0.5 cm filter paper strip soaked with fresh oat leaf juice and fitted into the upper end of the plastic straw. The inserted filter paper was pushed slightly aside in order to produce an open crevice between the tip of the "coleoptile" and the base of the "leaf". This crevice was sufficiently wide to permit the frit fly ♀ to insert the ovipositor and lay an egg.

In the first greenhouse experiment 200 uniformly distributed plant dummies were used as oviposition targets. In the second experiment 152 dummies were used with alternate dummies artificially infested with one frit fly egg, glued inside the tip of the "coleoptile" with a minute amount of a cellulose wallpaper paste. The remaining 76 dummies were controls and were only treated with the paste. In both these experiments about 300 frit flies were released into the cages for 24 hr to allow oviposition. Transparent plastic cylinders with nylon net tops were used as insect cages during the oviposition experiments with the food being a

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mixture of water, sucrose, and powdered milk (Le Berre *et al.*, 1961).

The effect of multiple ovipositions on the survival of larvae was studied by artificial inoculation of oat seedlings at the two-leaf stage with 1–3 frit fly eggs. After 3 weeks the plants were dissected and examined for pupae and larvae.

Results — The frequency distribution in the field plot is indicated in Table I. A total of 43 plants (21.5%) was used by the flies as egg-laying targets. The coefficient of dispersion (C.D.) was significantly higher than 1, which indicates a clear tendency towards an aggregation of eggs.

On the 200 untouched plant dummies, all eggs were laid inside the tip of the "coleoptile". The total number of dummies with eggs was 43 (21.5%). The C.D.-value was lower than in the field, but still significantly higher than that from a true Poisson distribution (Table I). In the second greenhouse experiment, oviposition resulted in 69 new eggs distributed on 35 dummies of which 27 came from the group with artificially added eggs and only 8 from the control group. This distribution indicates that dummies with an egg already present were preferred as oviposition targets. The deviation from the expected 1:1 distribution

was significant according to a G-test with Yates' correction (Sokal & Rohlf, 1969): $G_{adj} = 4.52$; $P < 0.05$.

The differences in larval survival rate between the 3 levels of infestation in the egg inoculation experiment were small and not statistically significant. However, under crowded conditions larvae tended to migrate from the main shoot to the newly formed tillers (Table II). Also larvae in plants randomly collected from a breeding cage showed a tendency towards a more uniform distribution. Here, 124 shoots were dissected and 56 larvae were found. The C.D.-value was 0.84, which is very low compared with the values obtained from egg distributions (Table I).

Discussion — When the frit fly ♀ searches the coleoptile region at the plant base for an egg-laying site, the extended ovipositor is very actively used. The tip of the ovipositor is turned from side to side, until a firm support is found. The inner surface of the coleoptile apex is the main target of this examination. Normally the narrow angle between the coleoptile edge and the leaf base offers a suitable support.

In order to receive eggs in a random manner, all plants must be equally attractive to the egg-laying flies, i.e., all coleoptiles must be in a suitable condition. This was probably not the

TABLE I

Statistical analysis of distribution data on eggs and larvae of *O. frit*. C.D. = coefficient of dispersion. Chi-squared tests made against expected Poisson distributions

	n	$\bar{y}$	C.D.	X^2	d.f.	P
Eggs on real oat plants (field)	200	0.36	2.04	16.32	1	<0.001
Eggs on plant dummies (greenhouse)	200	0.29	1.34	7.67	1	<0.01
Larvae in oat shoots (greenhouse)	124	0.45	0.84	0.83	1	n.s.

TABLE II

Distribution and survival of frit fly larvae in oat plants artificially inoculated with eggs

	No. of eggs per plant		
	1	2	3
No. plants	60	60	60
No. larvae and pupae	19	36	52
% survival	31.7	30.0	28.9
% plants with tillers attacked by larvae migrating from main shoot	14.3	20.7	53.3

case in the field, due to the normal variation between plants. Only plants with a disconnected coleoptile could be used as oviposition targets and with such a limitation in the number of available egg-laying sites, the chances must have been great that the same plants were selected repeatedly by the ♀♀. This was probably one reason for the contagious egg distribution in the field. In order to eliminate this source of error, plant dummies were used in the greenhouse experiments. In spite of the similarity between dummies, the results still showed a contagious egg distribution although it was less marked.

A preference of the ♀♀ to lay eggs on already occupied plants may be explained by the tendency of the ♀♀ to deposit their eggs at sites where a steady support for the ovipositor can be found. An egg attached to the inner surface of the coleoptile may offer such a support, which is indicated by the fact that the second egg is very often laid alongside the first one. Perhaps the presence of an egg thus provides a mechanically acceptable oviposition site on a plant, increasing the probability of further egg-laying.

Multiple ovipositions may seem maladaptive. The oldest egg will probably hatch first, and the first larva to invade the shoot will probably outcompete any intruder of the same species. Such an effect of competition is indicated in Table I, where the distribution of larvae in the shoots is shown to be less contagious than the corresponding distribution of eggs. Obviously the larvae are able to move from the

main shoot to a tiller, which is also shown in Table II. This ability of the larvae to move between shoots certainly reduces the disadvantage of multiple ovipositions. The secondary dispersal achieved in this way seems to compensate for the tendency of the ♀♀ to aggregate the eggs.

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Susceptibility of oat seedlings to oviposition by the frit fly, *Oscinella frit* L. (Dipt., Chloropidae)

By TH. JONASSON

Abstract

The susceptibility to oviposition by *Oscinella frit* in 16 oat cultivars was experimentally analysed in field and laboratory studies. The pattern of coleoptile withering and the corresponding separation of the coleoptile from the plant base was found to be of vital importance to the rate of oviposition. The oat seedlings were maximally attractive to the ovipositing females during the

early stage of coleoptile disconnection, when the eggs could be conveniently deposited in the narrow crevice between the plant base and the coleoptile. The probability of a certain cultivar being utilized for egg-laying was approximately proportional to the duration of a suitable coleoptile crevice. Oat cultivars with thin-walled and rapidly withering coleoptiles were more liable to escape frit fly attack than were cultivars with thick-walled and persistent coleoptiles. A high density of trichomes on the plant base surface did not entail any significant deterrent effect on egg-laying frit fly females.

1 Introduction

In southern Sweden late sown oat crops often suffer from heavy frit fly attacks. Indeed, early sowing in the spring is a good precautionary measure against the frit fly and also the cheapest way of minimizing the risk of an attack. In some areas in southern Sweden, however, spring sowing is often delayed due to wet conditions.

The lack of suitable insecticides and difficulties in predicting the time of oviposition disqualify chemical control of the frit fly as a routine practice. The most satisfactory method of control would therefore be the development of cultivars possessing a higher degree of resistance to this pest.

According to field results reported by several authors, there are significant differences in susceptibility to attack among oat cultivars. CUNLIFFE and HODGES (1946) and BINGHAM and LUPTON (1958) concluded, however, that the different levels of attack reflect different levels of oviposition on different oat cultivars.

The preference of the frit fly for oviposition behind the coleoptile has been stressed by several authors. ZHUKOVSKII (1932) stated that the coleoptiles of resistant wheat cultivars were, as a rule, tightly appressed to the stem, making oviposition impossible. ANDERSSON (1956) concluded that varietal differences in attractiveness for egg-laying in oats were mainly due to differences in the length of the period during which the coleoptile was offering a suitable site for oviposition.

Occasionally eggs are laid in the soil at the base of the host plant. According to ethological studies (JONASSON 1977), however, oviposition behind the disconnected coleoptile is the ordinary procedure, i. e. eggs are normally laid in the soil only if the female is unable to locate a suitable egg-laying site on the plant itself. In addition to the unsuitable coleoptile condition, another factor possibly associated with reduced preference to oviposition, according to ANDERSSON (1956), is the pubescence of the oat shoot bases.

In the present study the significance of the coleoptile disconnection pattern and the shoot base pubescence in connection with frit fly resistance is examined experimentally.

2 Materials and methods

The main part of the investigation was performed in the greenhouse. The frit flies used in the experiments were obtained from a culture maintained in the greenhouse described in JONASSON (1977). The test plants were cultivated in a standardized peat soil mixture in 25 cm plastic buckets or in 8 cm plastic pots. Transparent plastic cylinders provided with nylon net tops were used as insect cages.

In the series of experiments intended to give information on the rates of oviposition on the 16 cultivars, the plants were sown at a rate of about 50 seeds/bucket. The flies were introduced into the cages 10 days after sowing and they were confined there for 6 days. 16 flies were used in each

cage. All plants within the cages belonged to the same cultivar, i. e. the flies had no choice between different oat cultivars. Due to lack of space in the greenhouse the experiment was performed as a sequence of comparisons. Two test cultivar and one control (cv. Victory) were tested in each set, except in the last one, where only one test cultivar (Sang) and the control were used. In this way 16 oat cultivars were tested in three replicates. After the oviposition period the plants were examined for eggs behind the coleoptile.

In the preference experiment one plant each of the three cultivars; Victory, Risto, and Hede; were planted together in 8 cm plastic pots (20 replicates) and presented to 6 ovipositing flies for 3 days. Among the three cultivars tested in this free-choice experiment Hede has a high density of trichomes on the basal part of the plant. Two kinds of trichomes are present on cv. Hede: 1. short and hooked ones, which make the plant surface rough, and 2. long, straight ones, which make the plant surface hirsute. The cultivars Victory and Risto only have a low frequency of short trichomes and the long ones are completely absent. In order to make all plants equally available to oviposition behind the coleoptiles, the coleoptiles were artificially separated from the plant bases prior to the test.

Studies on the coleoptile disconnection pattern were made on plants sown in small plastic pots in the greenhouse. According to measurements made on living frit flies, the basal width of the ovipositor was about 0.3 mm. Therefore, judging from the egg-laying behaviour of *O. frit*, the coleoptile crevice was considered suitable for oviposition if it was greater than 0.3 mm. This measure was obtained by means of a metal wire, which was carefully inserted behind the coleoptile. The ability of the coleoptile to attract ovipositing females was considered to be lost when the interspace between the straw and the coleoptile was greater than 3 mm. At this stage most coleoptiles were wilted, and under field conditions they would probably have fallen to the ground. The coleoptile crevice of the test plants was measured once a day during the critical separation phase.

Observations in the field were made in small plots (1.25 × 2.80 m) drilled in four randomized blocks. In order to get a sufficiently high level of infestation, the plots were deliberately sown late. The result of the attack was assessed by means of visual inspection at an early developmental stage of the plants. In this way the possible influence of eggs laid after the critical coleoptile separation phase was restricted.

3 Results

The proportion of plants with disconnected coleoptiles 12 days after sowing, i. e. in the initial stage of the separation phase, are given in table 1. The results are given as indices relative to cv. Victory (Victory = 100; actual value = 16.7 %). Table 1 also gives the relative proportion of plants with eggs behind the coleoptile after an oviposition period of 6 days. In all sets of comparisons the index of cv. Victory is 100. The range of actual values was 16.1–34.2 % (mean = 22.6 %). An analysis of the two sets of data yielded the correlation coefficient $r = +0.92$ ($df = 14$; $P < 0.001$), indicating a very good correlation.

The results from the field experiment are listed in table 1 together with the mean persistence of the coleoptile crevices. There was a good correlation between coleoptile crevice availability to oviposition and the proportion of damaged main shoots ($r = +0.79$; $df = 14$; $P < 0.001$).

In table 2, the results from the free-choice experiment are given. Almost all eggs were laid either behind the coleoptiles or in the soil at the plant bases. The relative frequencies of coleoptile eggs and soil eggs were 60 % and 39 %, respectively. The remaining 1 % were attached freely on the plant surface. Hede, the cultivar with the highest density of trichomes on the shoot bases, received the smallest number of coleoptile eggs and a higher number of soil eggs than cv. Risto. It was, however, not possible to detect any significant difference in oviposition attractivity between the three cultivars tested (table 2).

Table 1. A compilation of results from greenhouse and field experiments

cultivar	Rel. proportion of plants		Mean proportion (%) of plants with attacked main shoot (field)	Mean persistence (d) of col. crevice (0.3–3 mm) (greenhouse)
	with col. crevice > 0.3 mm (greenhouse)	with eggs behind coleoptile (greenhouse)		
Victory	100.0	100.0	68.5	5.6
Condor	31.1	35.8	55.8	5.6
Sv 68322	40.1	52.3	63.0	5.9
Hede	51.5	47.2	39.0	4.3
Titus	101.2	72.0	63.0	5.8
Gotland oats	109.6	156.8	76.0	5.9
Sörbo	115.0	120.2	68.3	7.0
Spet	185.7	185.2	46.8	4.1
Linda	40.7	48.4	66.3	5.6
Summer	83.9	79.8	28.8	4.4
Risto	61.7	103.2	73.0	5.9
von Lochow's yellow oats	49.7	62.2	44.5	4.6
Sun II	30.0	29.6	48.3	4.8
Eagle	19.8	26.4	46.0	4.3
Selma	31.7	39.1	52.0	6.0
Sang	20.4	46.4	56.8	4.8
LSD _{0.05}	—	—	16.5	0.8
r	+ 0.92***		+ 0.79***	

LSD_{0.05} = Least significant difference at the 5 % level; r = correlation coefficient;
 *** = P < 0.001.

Table 2. Number of eggs per plant in a free-choice experiment in the greenhouse. The analysis of variance was performed with egg numbers transformed by $\sqrt{x + 0.5}$

No. of eggs per plant	Victory		Risto		Hede	
	range	mean	range	mean	range	mean
col. eggs	0–21	4.65	0–12	4.55	0–14	3.70
soil eggs	0–14	3.20	0–11	2.20	0–13	3.10
total	0–24	7.85	2–14	6.85	0–17	6.90

Source of variation	df	MS	Col. eggs		MS	Soil eggs		MS	Total	
			F	P		F	P		F	P
Replicates	19	1.459	1.808	>0.05	0.955	2.200	<0.05	1.441	2.320	<0.05
Cultivars	2	0.371	0.460	>0.50	0.439	1.012	>0.25	0.130	0.209	>0.75
Error	38	0.807			0.434			0.621		

4 Discussion

In a previous paper (JONASSON 1977) the interaction of different host plant stimuli affecting the oviposition behaviour of *O. frit* was analysed. The tactile stimulus from a narrow crevice on the young plant (particularly the crevice between the coleoptile and the plant base) was found to constitute an important part of the total stimulus pattern.

The preference of the flies for laying eggs behind the disconnected coleoptile was clearly demonstrated in the present study. The good correlation between coleoptile crevice availability and oviposition frequency ($r = +0.92$, tab. 1) indicates that the flies were able to locate the suitable oviposition sites very efficiently. It also indicates that the deterrent effect, if any, of hirsute or pubescent plants must have been very small. Among the cultivars tested the three old Scandinavian forms Summer, Spet, and Hede all have a high density of trichomes on the basal part of the shoot. Similarly, according to the free-choice experiment, the ovipositing flies did not seem to avoid the hirsute cv. Hede to any significant degree (table 2).

The good correlation between coleoptile crevice persistence and main shoot attack in the field ($r = +0.79$, tab. 1) is interesting. It might imply, in accordance with JEPSON and SOUTHWOOD (1958), that soil oviposition was of minor importance under field conditions. A study on the occurrence of coleoptile eggs in a late sown field plot of young oats (cv. TITUS) showed that almost all plants with main shoot damage had been subjected to oviposition behind the coleoptile. A total of 200 plants were examined. 175 (88%) plants showed symptoms of main shoot attack. Among these attacked plants 169 (97%) were provided with coleoptile eggs, whereas only 8 (32%) of the still unattacked plants had eggs in the coleoptile crevice. This indicated a strong association between coleoptile egg occurrence and main shoot damage ($V = +0.67$; $\chi^2 = 89.62$; $df = 1$; $P < 0.001$).

Although the frequency of soil eggs may sometimes be high even in the field, larvae hatching from these eggs run a considerable risk of being detected by predators. Therefore, the capacity to invade the host plant is lower in larvae hatching from soil eggs than in larvae hatching from coleoptile eggs (JONASSON 1977).

Varietal differences in susceptibility to frit fly attack in the seedling stage seemed to be closely dependent on the coleoptile disconnection pattern, quite in accordance with the results of ANDERSSON (1956). The differences in oviposition rates obtained from the greenhouse experiment (tab. 1) are not directly comparable with the different proportions of main shoot attack in the field experiment (tab. 1). This is because the greenhouse experiment only covered the initial phase of the susceptible stage of the test plants. Although the results are to only be considered as "snapshots", they clearly indicate that the plants were maximally attractive to oviposition when there was a narrow crevice between the coleoptile and the plant base. Since all oat plants have to pass through this critical stage of susceptibility to frit fly oviposition, plants with rapidly disconnecting coleoptiles should run the lowest risk of becoming targets for the ovipositing flies, as indicated in the field experiment.

When searching for cultivars possessing a higher degree of frit fly resistance of the non-preference type (PAINTER 1951), the desirable coleoptile characters would be relatively simple to select for. It must be emphasized, however, that resistance to oviposition is, without a doubt, only part of a complex of mechanisms involved in oat plant resistance to frit fly attack. Further studies are needed, for example, to find out to what extent oat cultivars are able to resist penetration by frit fly larvae.

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Zusammenfassung

Zur Empfindlichkeit von Haferkeimlingen auf die Eiablage der Fritfliege, Oscinella frit L. (Dipt., Chloropidae)

Im Freiland und Gewächshaus wurde die Empfindlichkeit von 16 verschiedenen Hafersorten gegenüber der Eiablage der Fritfliege untersucht. Es zeigte sich, daß das Absterben der Koleoptile und die damit verbundene Hohlraumbildung zwischen Koleoptile und Stengelgrund von entscheidender Bedeutung für die Eilegerate war. Die Haferkeimlinge waren für die eierablegenden Weibchen während des 1. Stadiums des Koleoptilenabsterbens am attraktivsten. In diesem Stadium war es leicht für die legebereiten Fliegen, die Legeröhre zwischen die Koleoptile und den Stengelgrund einzupressen. Die Anfälligkeit einer bestimmten Sorte zur Fritfliegen-Eiablage war ungefähr proportional der Dauer des Koleoptilenabsterbens. Haferpflanzen mit dünneren und schneller absterbenden Koleoptilen waren für den Fritfliegenbefall weniger geeignet als solche mit dickeren und langsamer absterbenden Koleoptilen. Eine hohe Dichte von Haaren der Halmoberfläche hatte keine merkbare abweisende Wirkung auf eierablegende Fritfliegen.

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Resistance of oat plants to larval attack by the frit fly, *Oscinella frit* L. (Dipt., Chloropidae)

By TH. JONASSON

Abstract

Greenhouse experiments showed that oat cultivars known to differ significantly with regard to frit fly attack in the field were almost equally susceptible to larval penetration at an early developmental stage. All cultivars became more resistant with increasing age, the level of resistance, however, being significantly different among the cultivars.

Oat cultivars known to be relatively resistant in the field were the most susceptible in the greenhouse and vice versa. This seemingly inconsistent result was probably due to a negative relationship between resistance to oviposition and resistance to larval penetration among the cultivars studied.

1 Introduction

The frit fly is a severe pest of oats in southern Sweden. In some areas the crop losses due to this insect normally exceed 10 % annually. Although efficient insecticides are now available, new oat cultivars with higher degrees of resistance are desirable for a satisfactory solution to the frit fly problem.

According to experimental results reported by several authors, the variation in susceptibility among oat cultivars is wide enough to raise hopes for successful plant breeding work. CUNLIFFE and HODGES (1946), BINGHAM and LUPTON (1958), and PEREGRINE and CATLING (1967) have all investigated the possibilities of such a breeding programme. Their general conclusion was that resistance to frit fly attack is associated with a low attractivity for oviposition.

ZHUKOVSKII (1932), RIGGERT (1935), ANDERSSON (1956), and SANDERS (1960) pointed out that the frit fly female prefers to lay eggs inside the loose coleoptile of cereal seedlings. Experimental data (JONASSON 1980) accordingly showed that there was a good correlation between the pattern of coleoptile development in a series of oat cultivars and the relative attractivity for oviposition.

The egg-laying behaviour and the mechanisms of host plant selection in the female frit fly have been studied experimentally by IBBOTSON (1960), SANDERS (1960), and JONASSON (1977), but very little is known about the behaviour of the larvae. CUNLIFFE (1936) suggested that a large proportion of crude fibre in the plant was associated with resistance to larval penetration, and DORFSCHMID (1952) found differences in the content of cellulose and pectin in young plants of different oat cultivars. CUNLIFFE and HODGES (1946), however, concluded that the resistance of oat plants was not correlated with the carbohydrate content.

Failures to demonstrate direct resistance to larval penetration are possibly due to the fact that preferential oviposition has a dominating influence on the total result in most field experiments with *Oscinella frit*. The purpose of the

present study was therefore to eliminate, or at least reduce, the effect of differences in frit fly oviposition among different oat cultivars and to find out if there are differences in resistance to larval penetration.

2 Materials and methods

Larval attack in different oat cultivars at different developmental stages was studied in a greenhouse experiment. Eight cultivars (table 1) known to differ significantly with regard to frit fly attack in the field were sown in peat soil in 25 cm plastic buckets at a rate of about 50 plants/bucket. All plants within a bucket were of the same cultivar. Sixteen newly emerged frit flies in a sex ratio about 1:1 were introduced to the plants 10, 16, 22, and 28 days after sowing, and the plants were exposed to oviposition for six days. Transparent plastic cylinders with nylon net tops were fitted into the buckets and used as insect cages. The adult flies were fed with a mixture of water, sucrose, and powdered milk according to LE BERRE *et al.* (1961) during the confinement in the cages. Two weeks after egg-laying larval damage to the plants was assessed.

Resistance to larval penetration in the cultivars Hede and Gotland was studied by artificial inoculation of 67 plants/cultivar (15 days after sowing) with one frit fly egg each.

The experiments were performed in a greenhouse at 20–22 °C, 16 h light period. Frit flies were obtained from a culture established with specimens collected from infested oat panicles and maintained on oat plants in the greenhouse for 6–7 generations.

Table 1. Origin and year of release of the oat cultivars used in the experiment

Cultivar	Origin (year of release)
1. Hede	Old local form from Jutland, W Denmark
2. Spet	Old local form from Småland, S Sweden
3. Summer	Old local form from Gotland, SE Sweden
4. Gotland	Old local form from Gotland, SE Sweden
5. Victory	Selection from Probststeier oats, Svalöf (1908)
6. Sörbo	Modern cultivar, Svalöf (1967)
7. Selma	Modern cultivar, Weibullsholm (1970)
8. Sang	Modern cultivar, Svalöf (1974)

Table 2. Plant damage by frit fly larvae ($\bar{X} \pm 1$ S.E.). Each mean value is based on 10 replicates. The analysis of variance was performed with percentages transformed by $\arcsin \sqrt{p}$ (angular transformation)

Cultivar/damage in %	Plant age = number of days after sowing			
	10	16	22	28
1. Hede	76 $\pm$ 7.4	79 $\pm$ 4.3	71 $\pm$ 6.6	58 $\pm$ 6.6
2. Spet	69 $\pm$ 8.1	68 $\pm$ 6.9	66 $\pm$ 7.5	43 $\pm$ 5.0
3. Summer	66 $\pm$ 8.1	61 $\pm$ 8.3	61 $\pm$ 5.6	40 $\pm$ 5.5
4. Gotland	66 $\pm$ 7.6	50 $\pm$ 6.9	36 $\pm$ 5.7	24 $\pm$ 6.3
5. Victory	64 $\pm$ 8.7	68 $\pm$ 7.2	47 $\pm$ 7.7	17 $\pm$ 4.5
6. Sörbo	68 $\pm$ 8.6	63 $\pm$ 8.2	50 $\pm$ 6.9	21 $\pm$ 5.7
7. Selma	73 $\pm$ 4.8	69 $\pm$ 9.9	61 $\pm$ 6.4	34 $\pm$ 6.1
8. Sang	62 $\pm$ 8.9	75 $\pm$ 5.6	42 $\pm$ 8.5	14 $\pm$ 2.9
Source of variation	df	MS	F	P
Cultivars (A)	7	1415.9	6.638	< 0.001
Plant age (B)	3	9882.0	46.329	< 0.001
Interaction (A $\times$ B)	21	254.2	1.192	ns
Error	288	213.3		

3 Results

The proportion of plants with larval damage is given in table 2 and the figure. In the early seedling stage (10 days after sowing) all cultivars were almost equally susceptible to larval attack. Already in the early three-leaf stage of the plants (16 days after sowing), however, a significant variation in susceptibility among the cultivars appeared. This variation became even more obvious at later stages of plant development. The absence of interaction (table 2) indicates that the trend is the same in all cultivars: resistance to larval attack increases with increasing plant age.

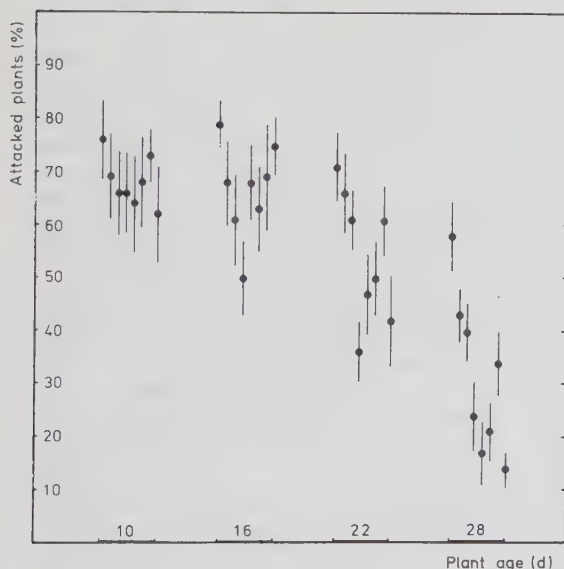


Fig. 1. Plant damage by frit fly larvae. Graphical illustration of data from tab. 2. The cultivars are arranged 1-8 from left to right in each set according to the numerical order used in tab. 1-2. Each point refers to $\bar{x} \pm 1$ S.E.

The artificial inoculation of seedlings with frit fly eggs showed that Gotland was more resistant to larval penetration than Hede. Thirty-three Gotland plants (49 %) and 46 Hede plants (69 %) were attacked, the difference being statistically significant according to a G-test with Yates' correction (SOKAL and ROHLF 1969): $G_{adj} = 4.47$; $P < 0.05$.

4 Discussion

In the greenhouse experiment the flies had no choice between different cultivars, and differences in egg-laying preference therefore presumably did not influence the results. Probably there were differences among the cultivars in coleoptile development during the oviposition period starting 10 days after sowing (cf. JONASSON 1980), but in later stages all coleoptiles were disconnected and equally attractive to the egg-laying flies. It can therefore be concluded that differences in frit fly attack were mainly due to different levels of resistance to larval penetration. The occurrence of resistance to larval attack

was also confirmed by the artificial inoculation of Hede and Gotland plants with frit fly eggs.

Hede, Spet, and Summer are old Scandinavian forms known to possess a relatively high level of resistance to frit fly attack in the field (CUNLIFFE 1929). The other five cultivars (table 1) are highly susceptible, at least when sown late. Victory was used by CUNLIFFE (1929, 1936) and CUNLIFFE and HODGES (1946) as a susceptible control in several field experiments. Surprisingly, the cultivars known to be resistant in the field were the most susceptible in the greenhouse experiment and vice versa. This seemingly inconsistent result may be explained if resistance to oviposition and resistance to larval penetration are analysed separately. The reactions of Hede and Gotland under field and greenhouse conditions can be used as an example: In the field experiment (JONASSON 1980) 39 % of the Hede plants and 76 % of the Gotland plants were attacked. In the egg inoculation experiment in the greenhouse, however, 69 % of the Hede plants and only 49 % of the Gotland plants were attacked. The field experiment was sown late. This means that a large number of ovipositing flies were active during the initial phase of the coleoptile separation, when varietal differences in oviposition attractivity occurred but differences in resistance to larval penetration presumably were insignificant. The result of the attack was assessed at an early developmental stage of the plants, which restricted the possible influence of eggs laid after the critical coleoptile separation phase. In short, differences in larval attack in the field were mainly due to differences in oviposition attractivity. In the greenhouse experiment, however, with artificial inoculation with eggs, oviposition preference was eliminated. Hence, the result shows the effect of different levels of resistance to larval penetration.

Hede, Spet, and Summer all have thin, rapidly wilting coleoptiles which only offer suitable sites for oviposition for a short period. These cultivars are therefore more liable to escape egg-laying in the field (ANDERSSON 1956, JONASSON 1980). Sörbo and especially Gotland, however, are more susceptible to oviposition because of persistent, thick coleoptiles. During the initial phase of the coleoptile separation (about the two-leaf stage) all plants seem to be very susceptible to larval penetration, oviposition in the field normally starting at this stage. Later on, however, the resistance to penetration gradually increases, which consequently implies that larvae hatching from eggs deposited during the final stage of the coleoptile separation may have difficulties in entering the host plant. Field results (JONASSON in prep.) similarly indicate that the overall level of frit fly attack is due to an interaction of resistance to oviposition and resistance to larval penetration. Under different conditions the relative importance of these two factors may change and hence give results which are difficult to interpret.

From a practical point of view, the aim of the breeding work within a frit fly resistance programme should be to bring about a combination of low attractiveness for oviposition and a high level of resistance to larval penetration in the same oat cultivar.

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Zusammenfassung

Resistenz von Haferpflanzen gegen den Befall durch Larven der Fritfliege, *Oscinella frit* L.
(Dipt., Chloropidae)

Gewächshausexperimente ergaben, daß Hafer-Kultivare, die im Freiland unterschiedlich signifikant auf Fritfliegen-Eiablage reagierten, die gleiche Empfindlichkeit hinsichtlich der Schädigung junger Pflanzen durch Fritfliegen-Larven zeigten. Alle Kultivare wurden mit zunehmendem Alter resistenter, wobei jedoch der Resistenzgrad zwischen den Kultivaren verschieden war. Hafer-Kultivare, die sich im Freiland relativ resistent zeigten, waren im Gewächshaus am empfindlichsten und umgekehrt. Dieses scheinbar widersprüchliche Ergebnis beruhte wahrscheinlich auf einer negativen Beziehung zwischen der Resistenz gegen die Eiablage und jener gegen das Einbohren von Larven.

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THE INTERACTION OF OVIPOSITION AND LARVAL PENETRATION
IN RESISTANCE TO FRIT FLY, OSCINELLA FRIT,
IN OAT SEEDLINGS (DIPT., CHLOROPIDAE)

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ABSTRACT

Field and greenhouse experiments indicate that frit fly resistance in oat seedlings consists of 1) resistance to oviposition and 2) resistance to larval penetration. The two components act at different development stages of the young plants. The level of resistance, as observed in field experiments, is normally the sum effect of both factors. The relative contribution to the sum effect from each of them may differ under different conditions. In late sown plots, where the frit fly attack starts during the early development stages of the seedlings, resistance to oviposition tends to dominate, since varietal differences in oviposition attractivity are most markedly expressed in young seedlings. In early sown plots, however, where the oat seedlings are older when the attack starts, resistance to larval penetration seems to be more important in the final expression of resistance to frit fly attack. Under normal conditions of cultivation, resistance to larval penetration is the most important mechanism. This character should therefore be given a high priority in attempts at breeding frit fly resistant oat cultivars.

INTRODUCTION

The frit fly Oscinella frit (L.) is a common pest of oats in southern Sweden. In late sown crops the stem boring larvae may cause severe damage when attacking the seedlings.

A close relationship between attractivity for egg-laying and susceptibility to attack among oat cultivars was pointed out by Cunliffe and Hodges (1946), Bingham and Lupton (1958), and Peregrine and Catling (1967). The frit fly female prefers to lay her eggs in the narrow crevice behind the loose coleoptile of cereal seedlings (Riggert 1935, Andersson 1956, Sanders 1960). Andersson (1956) reported from studies in oats that varietal differences in oviposition attractivity were largely due to differences in the length of the period during which the coleoptile offered a suitable site for oviposition. Jonasson (1980) similarly reported experimental data showing a good correlation between the pattern of coleoptile development and the relative susceptibility to oviposition in a series of oat cultivars.

Although different rates of oviposition among oat cultivars have a great influence on the final expression of resistance to frit fly attack, other mechanisms of resistance appear to be involved in the frit fly - oat seedling interaction. Jonasson (1982) reported evidence of differences in direct resistance to larval penetration among oat cultivars. This paper attempts to analyse experimentally the effects of differential oviposition and differential larval penetration in the final expression of frit fly resistance in oat seedlings.

MATERIAL AND METHODS

Varietal differences in frit fly attack were studied in a series of field experiments at Svalöf. The material chosen for the study comprised both modern cultivars and old local types of Scandinavian origin, several of which were classified by Cunliffe (1929) as being either particularly resistant or susceptible to frit fly attack. The experiments were performed in four randomized blocks, with plot size 1.25 x 2.80 m. A total of 10-20 cultivars were included in each experiment. To increase the probability of heavy attacks, sowing was in most cases deliberately delayed. The results of the frit fly attacks were assessed by counting the number of dead main shoots on 25 consecutive plants, in four sites, diagonally across each small plot.

The cultivars Summer, Selma, Victory, Sörbo, and Gotland were sown together in single rows in a randomized sequence under 1.3 x 1.3 x 1.3 m frit fly proof nylon net cages in the field. Two sowing dates, with an interval of one week were used, each consisting of 9 replications. When the plants from the later sowing date were at the one-leaf stage, all cages were simultaneously removed. The older plants had then reached an early three-leaf stage. All plants were therefore exposed to the egg-laying frit flies in the field at the same time. When the symptoms of attack became clearly visible about two weeks after exposure, the number of dead main shoots were recorded.

A series of cage experiments in the greenhouse was also performed with the cultivars Summer, Selma, Victory, Sörbo, and Gotland in order to estimate varietal differences in oviposition attractivity, and resistance to larval penetration at two development stages in the plants. Sixteen newly emerged flies of a sex ratio about 1:1 were introduced into each cage when the plants were 10 or 16 days old. Sowing occurred in 25 cm plastic buckets filled with peat soil at a rate of about 50 seeds/bucket. All plants within a bucket were of the same cultivar and the same age. Transparent plastic cylinders fitted to the buckets were used as insect cages during the egg-laying period. The flies were kept in the cages for 6 days. The first eggs were normally laid after 2 days and therefore the actual oviposition period was only 4 days (12-16 and 18-22 days after sowing, respectively). After the oviposition period all plants were examined for eggs behind the coleoptile. Two weeks later larval attacks on the plants were assessed. The experiments were carried out as a series of comparisons,

where cv. Victory always was used as a control. Four replications were used for each plant age and each cultivar. Since each replication was always accompanied by a corresponding set with cv. Victory, all results were treated as indices relative to the control (cv. Victory = 100).

RESULTS AND DISCUSSION

In Fig. 1 the results of 12 field trials 1975-77 are presented in rough outline. The results clearly demonstrate the strong influence of sowing date on the overall level of frit fly attack. It is a well known fact that the risk of attack increases if sowing is delayed. The illustration also shows that resistance to frit fly is a relative concept. The most resistant cultivars had a high percentage of attacked main shoots when sowing was very late. The largest differences in attack among the cultivars were obtained at intermediate levels of attack. Summer, Hede, and Spet, all being pure line selections from old local cultivars from Scandinavia, were the least attacked (cf. Cunliffe 1929). The most severely attacked cultivars were Maris Oberon and Victory. Cunliffe (1929) reported cv. Victory as susceptible to frit fly attack. The cultivars Selma, Sang, Gotland, Sörbo, and von Lochow's Yellow occupy intermediate positions on the ranking scale. Highly significant differences in frit fly attack were obtained between cultivars in all 12 experiments included in Fig. 1.

Although the extreme cultivars, i.e. the most resistant and the most susceptible ones, held their positions on the ranking scale quite well throughout the field experiments, it is evident that several cultivars changed their positions from one experiment to another. This is illustrated in Tab. 1, where five oat cultivars from a total of 24 field experiments during the period 1973-77 are included. The table shows the relative ranking positions among the cultivars Summer, Sörbo, Gotland, Selma, and Victory. The most resistant cultivar, Summer, with its consistently low levels of attack, occupies a steady position at the top of the ranking list. The remaining cultivars are less stable. Cvs Gotland and Selma are the most remarkable, holding four different positions out of five possible, while cvs Sörbo and Victory oscillate between three. An essential question in this connection is whether the changing ranking positions are random irregularities between different experiments or if there is a pattern behind the phenomenon.

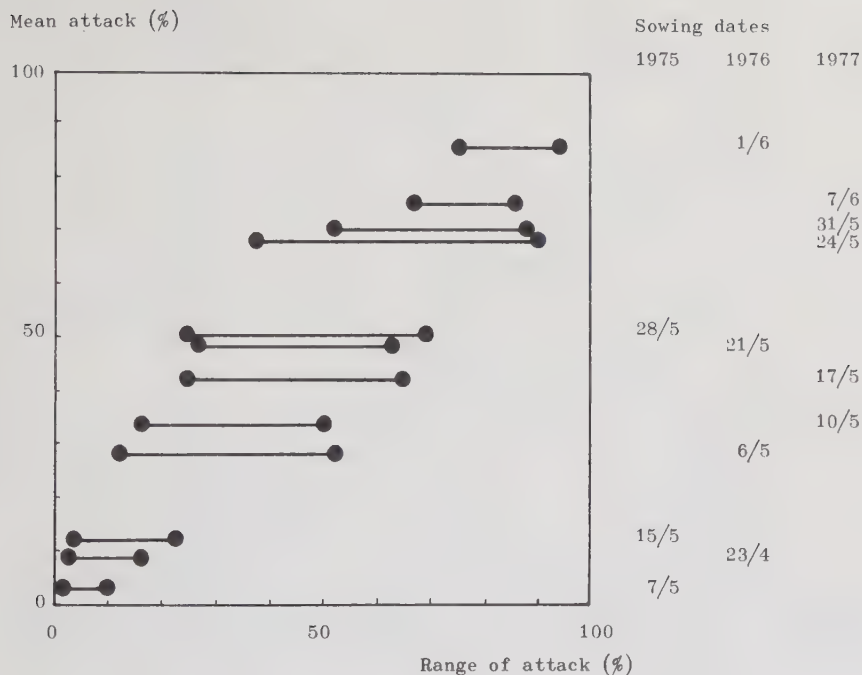


Figure 1. Mean and range of frit fly attack in 12 field trials including 10 - 20 oat cultivars sown at different dates 1975-77 at Svalöf.

Table 1. The frequency of different ranking positions among five oat cultivars in 24 field experiments carried out at Svalöf 1973-77.

Cultivar	Ranking position				
	1	2	3	4	5
Summer	22	2	0	0	0
Sörbo	2	19	3	0	0
Gotland	0	2	11	4	7
Selma	0	1	7	8.5	7.5
Victory	0	0	3	11.5	9.5

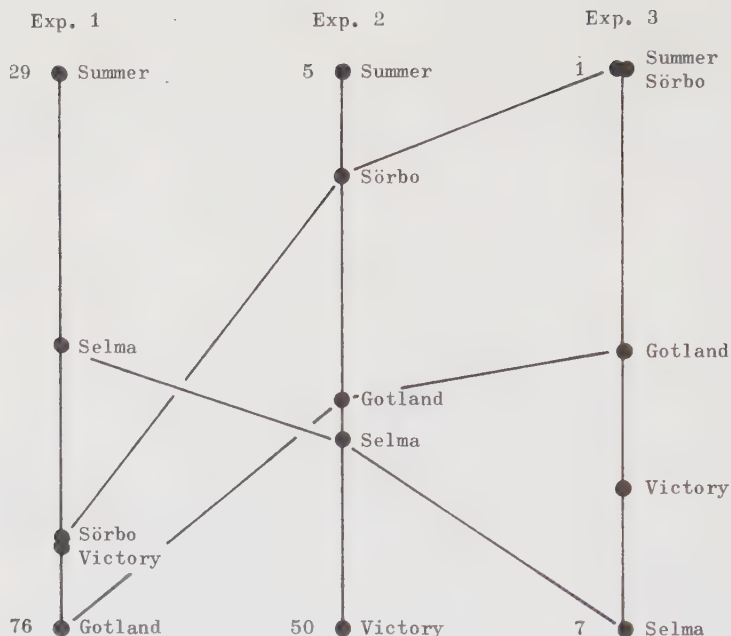


Figure 2. Five oat cultivars ranked according to frit fly attack in three different field experiments sown at a late (1), medium (2), and early (3) date. Figures indicate actual proportions (%) of attacked main shoots.

In Fig. 2 the five cultivars discussed above have been ranked on a relative scale of main shoot attack as observed in three field experiments clearly differing in sowing dates. In experiment 1 the sowing was very late and the seedlings were attacked at an early stage. In experiment 2 the plots were sown earlier and the attack was not so heavy, since the plants were older when the flies laid their eggs. In experiment 3 the sowing was earliest and the plants had almost passed the susceptible early developmental stages when the attack started. There seems to be a certain pattern in the changes of ranking positions among the cultivars. It appears that the developmental stage of the plants at the time of attack is important not only for the overall level of attack but also for the relative level of attack among the cultivars. A cultivar which is susceptible to attack at a late sowing date may turn out to be relatively resistant when sown early. As is shown by Fig. 2 this pattern applies to cvs Sörbo and Gotland. The reaction of cv. Selma, however, seems to be the very opposite; a moderate level of resistance at late sowing and susceptibility at early sowing.

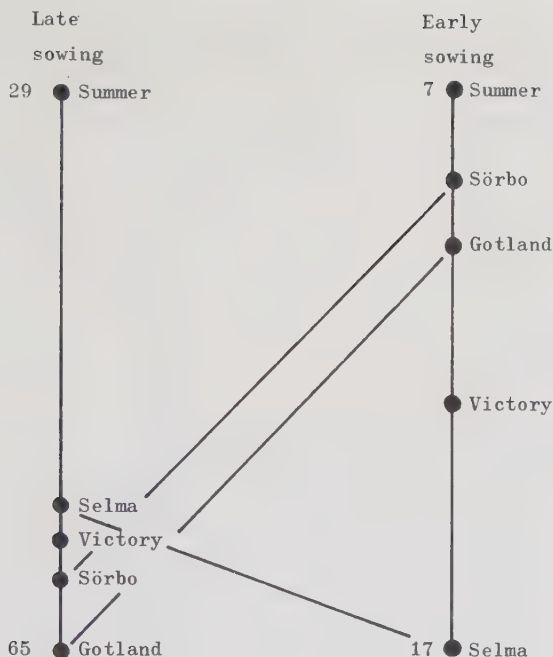


Figure 3. Same oat cultivars as in Fig. 2 ranked according to frit fly attack in a cage experiment in the field. The material was sown under frit fly proof cages at two sowing dates with an interval of a week. When the youngest plants had reached the one-leaf stage all cages were removed and the plants were simultaneously exposed to the frit fly population in the field. An analysis of variance is given in Tab. 2. Figures at ends of the relative scales indicate actual proportions (%) of attacked main shoots.

The hypothesis that the relative level of attack is influenced by the developmental stage of the plants at the time of attack was tested in a cage experiment in the field (see section Material and methods). The results are shown in Fig. 3 and Tab. 2. A regular pattern in the changes of the ranking positions of the cultivars was evident from the statistical analysis (Tab. 2) which illustrates the differences between sowing dates and cultivars. At the same time it shows that there is a significant interaction between sowing date and cultivar, indicating that the different reactions of the cultivars depend on the plant's development stage at the time of attack.

Table 2. An analysis of variance on the cage experiment illustrated in Fig. 3. Calculations were made with percentages transformed by $\arcsin \sqrt{p}$ (angular transformation).

Source of variation	d.f.	MS	F	P
Between cultivars (A)	4	576	13.4	< 0.001
Between sowing dates (B)	1	17763	413.7	< 0.001
Interaction A x B	4	232	5.4	< 0.001
Error	80	43		

The results of the greenhouse experiments (Fig. 4 and Tab. 3) show that two separate mechanisms affect the final expression of the frit fly attack. These two mechanisms act in sequence during the early stages of oat plant development. The first component is associated with differences in oviposition attractivity among the cultivars. These differences are expressed in the young plants only (Tab. 3A). The second component is associated with different levels of resistance to larval penetration among the cultivars. These differences, on the other hand, can only be observed in the older plants (Tab. 3D).

It may seem surprising that although there were significant differences in oviposition attractivity (expressed as the frequency of plants with eggs behind the coleoptile), there were no differences in larval attack among the cultivars during their early development. This effect was due to the large proportion of eggs laid in the soil around the plants. Egg-laying in the soil may be common under greenhouse conditions (Jonasson 1977) but is rare in the field (Jepson and Southwood 1958).

The most important information from the greenhouse experiment (Fig. 4 and Tab. 3) is that during the period of differentiated attractivity to oviposition all cultivars were equally susceptible to larval penetration and that during the period of differentiated resistance to larval penetration all cultivars were equally attractive as oviposition targets. This may explain the varying expressions of resistance obtained in field experiments. In late sown fields, where the plants are attacked at an early developmental stage, resistance to frit fly attack is mainly due to a low attractivity to the ovipositing females. If sowing is early, however, the plants are attacked in a more advanced stage of development and therefore the resistance observed is mainly due to a low penetration success by the larvae.

10-16 days
after sowing

16-22 days
after sowing

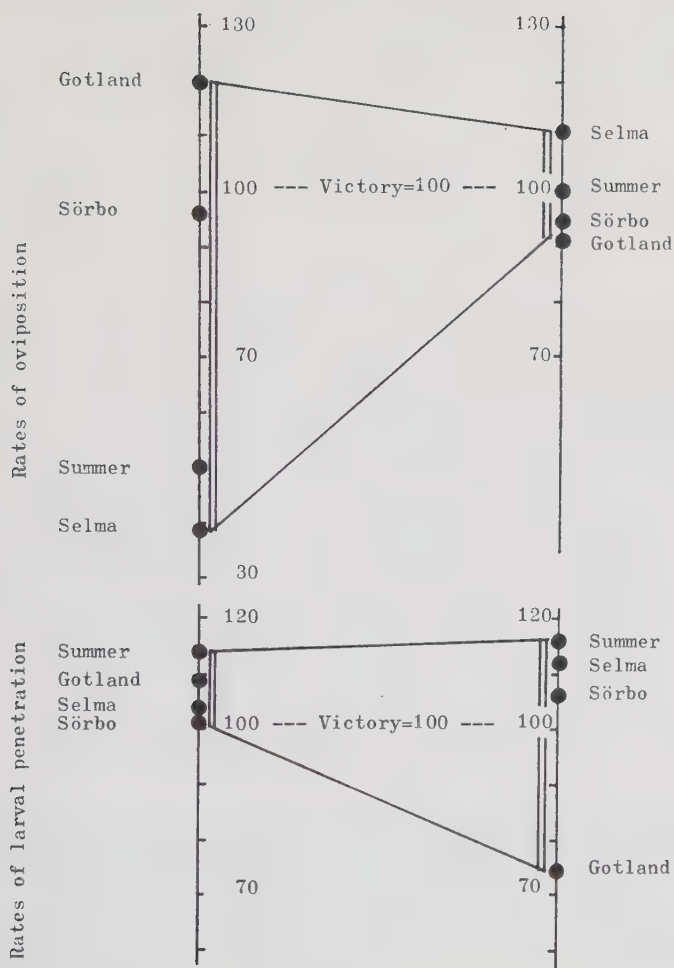


Figure 4. Relative rates of oviposition and larval penetration in different oat cultivars in two developmental stages. Graphical illustration of data from Tab. 3.

Table 3. Relative frequencies of plants with eggs behind coleoptile (A-B) and plants attacked by larvae (C-D). Oviposition periods: 10-16 (A,C) and 16-22 (B,D) days after sowing. Standard cultivar Victory = 100; Actual frequencies (%) for cv. Victory are given in brackets (mean $\pm$ S.E.M.; n = 16). Mean values within columns followed by different letters differ significantly according to Student-Newman-Keules test (P = 0.05).

A-B. Relative frequencies of plants with eggs behind coleoptile. Oviposition periods: 10-16 (A) and 16-22 (B) d after sowing.

A. Victory = 100 (28.1 $\pm$ 2.17)						B. Victory = 100 (72.1 $\pm$ 2.26)					
Cultivar	Frequency/replication					Frequency/replication					Mean
	1	2	3	4	Mean	1	2	3	4	Mean	
Selma	49	34	49	22	39a	92	140	110	103	111a	
Sörbo	119	85	118	61	96b	95	105	86	95	95a	
Gotland	104	169	123	84	120b	96	90	89	89	91a	
Summer	75	65	52	7	50a	99	107	103	92	100a	

C-D. Relative frequencies of plants attacked by larvae. Oviposition periods: 10-16 (C) and 16-22 (D) d after sowing.

C. Victory = 100 (80.3 $\pm$ 3.17)						D. Victory = 100 (71.6 $\pm$ 6.17)					
Cultivar	Frequency/replication					Frequency/replication					Mean
	1	2	3	4	Mean	1	2	3	4	Mean	
Selma	109	100	101	100	103a	118	106	100	119	111a	
Sörbo	104	94	114	93	101a	130	100	98	98	107a	
Gotland	117	110	96	112	109a	67	72	72	88	75b	
Summer	139	92	105	120	114a	134	131	88	110	116a	

It is interesting that cvs Summer and Selma were more resistant to oviposition than cvs Gotland and Sörbo in the early two-leaf stage (10 - 16 days after sowing). This is in accordance with data given by Jonasson (1980). It is also interesting that cv. Gotland was more resistant to larval penetration than cvs Summer, Selma, and Sörbo in the early three-leaf stage (16 - 22 days after sowing). An early resistance to larval penetration in cv. Gotland was also demonstrated by Jonasson (1982).

It is surprising that cv. Sörbo, which according to the field results (Tab. 1 and Fig. 2) would be expected to possess a high level of resistance to larval penetration, did not differ significantly from cvs Summer and Selma in this respect (Tab. 3D). In a previous study (Jonasson 1982), however, cv. Sörbo acquired a good resistance to larval penetration, although this resistance developed later than in cv. Gotland. Another sur-

Table 4. Tiller length in non-attacked plants with main shoot in early five-leaf stage. Sample size: 10 plants/cultivar. Mean values followed by different letters differ significantly according to Student-Newman-Keules test ($P = 0.05$). S.E.M. = Standard Error of Mean.

Cultivar	Length of tallest tiller in cm (mean $\pm$ S.E.M.)	
Summer	21.5 $\pm$ 0.52	a
Victory	15.4 $\pm$ 0.93	b
Sörbo	14.4 $\pm$ 1.11	b
Selma	14.3 $\pm$ 0.56	b
Gotland	13.2 $\pm$ 1.12	b

prising result is that cv. Summer, which obviously remains very susceptible to larval penetration (cf. Fig. 4 and Jonasson 1982), was the most resistant cultivar in most of the field experiments (Tab. 1). The explanation is probably the growth habit of cv. Summer. Summer, like many of the old local Scandinavian types, has an early production of tillers (Tab. 4). Cvs Sörbo, Gotland, Selma, and Victory have almost equally developed tillers, while those of cv. Summer are significantly taller, being about 50 % longer. Tillers produced early may attract the egg-laying frit fly females and possibly also the young larvae. Consequently the main shoot may escape attacks already at an early developmental stage.

CONCLUSIONS AND IMPLICATIONS FOR PLANT BREEDING

Complete frit fly resistance has never been reported in Avena. Partial resistance, however, has been described by several authors (Cunliffe and Hodges 1946, Bingham and Lupton 1958, Peregrine and Catling 1967). Lupton (1981) concluded with reference to the study by Bingham and Lupton (1958) that varietal differences in frit fly resistance are difficult to demonstrate and irregular in their expressions. My own study similarly shows that it may be difficult to obtain consistent results from series of field experiments. Sometimes the resistance to oviposition has a dominating influence on the final expression of resistance and sometimes the resistance to larval penetration has the greatest influence. In late sown experiments resistance to oviposition tends to dominate, whereas in early sown experiments resistance to larval penetration is more important.

In most field studies on frit fly resistance late sowing has been practised to increase the probability of a high level of attack. As a result the oviposition component of the total expression of resistance may have been exaggerated. Consequently, resistance to larval penetration may have been masked by a high susceptibility to oviposition. According to Jonasson (1982) there was an inverse relationship between resistance to larval penetration and resistance to oviposition in a group of eight oat cultivars studied. If such a general negative correlation between the two components exists, the evaluation of field test results may be very complicated. From a practical point of view, however, resistance to oviposition seems to be less important. In most regions of Sweden the oat crop can be sown early enough to escape attacks by Oscinella in the early seedling stage. When damage occurs, it is normally caused by larvae invading the plants at a stage when resistance to larval penetration starts to develop. Therefore an early expression of resistance to larval penetration appears to be the most important character to be selected for when breeding oats for a higher degree of frit fly resistance.

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